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Examining the natural history and biogeography of an endemic timberline pine (Pinus balfouriana)

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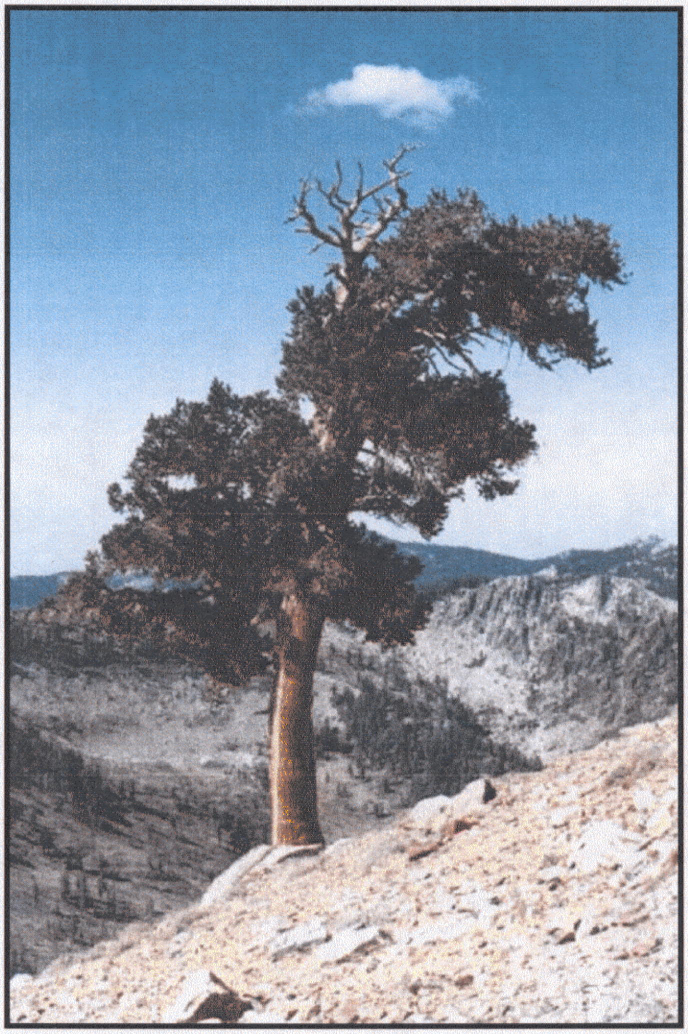

A Capstone Project Presented to the Faculty of
Earth Systems Science and Policy
in the
Center for Science, Technology, and Information Resources
at
California State University, Monterey Bay
in Partial Fulfillment of the Requirements for the Degree of
Bachelor of Science

By Michael Bogan
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April 21, 2001

To the faculty of ESSP:

The foxtail pine (*Pinus balfouriana* spp. *austrina*) is a subalpine pine species endemic to the Southern Sierra Nevada of California. Due to its relative inaccessibility, the species has been studied little and its ecological characteristics and evolutionary history are not well understood. The tree's longevity (up to 3300 years) is very useful to the paleoclimatic studies, as the tree's annual growth-ring record can yield clues to past climatic conditions in the Sierra Nevada and elsewhere. The Sierran foxtail pine has a northern relative (spp. *balfouriana*); the two groups haven arisen through allopatric speciation, but are now separated by over 500 kilometers. In this capstone study, the Sierran foxtail's ecological characteristics were studied at 3 sites along the margin of its narrow range, and at 1 site in the central part of its range. In addition, a raw ring-width database of tree-ring cores was examined to look at paleoclimatic conditions for those sites, and to examine past climatic trends to see if current resource-based policies are adequate for climatic conditions other then those at present. This project was significant as a baseline study for creating hypotheses that could be used in further studies. Additionally, data gathered and processed for this study can be used for future scientific sampling at the four study sites to make more definitive conclusions about how and why the Sierran foxtail came to be in its present distribution.

In this study I had the opportunity to work with many knowledgeable professionals outside the realm of ESSP. First and foremost was Connie Millar, a forest geneticist with the United States Forest Service. Connie has spent most of her career studying the evolution, paleoecology and genetic structure of trees, including redwoods, whitebark pines, and Monterey pines. She is extremely well versed in multiple fields, and is what ESSP graduates should aspire to be. Connie was helpful in brainstorming, making contacts, and offering the use of the USFS genetics lab in Albany, CA. Though the genetics work originally proposed in this capstone was not done, it is planned for completion as part of another capstone in fall 2001. Connie's enthusiastic assistance for an undergraduate-level study was greatly appreciated. Andrea Lloyd, now of Middlebury College, was also helpful to the study. She examined foxtail pines as part of her Ph.D. dissertation on timberline fluctuation in the Southern Sierras. Andrea assisted by sharing resources and copies of her own studies. Deborah Rodgers, a conservation biologist and research geneticist at UC Davis, also contributed feedback to my capstone study and sent copies of relevant field and lab work that she had conducted.

The results of this project are intended for several groups of people. First, this project is of interest to those in the field of evolutionary biology. The *Balfourianae* group of pines (consisting of the two foxtail pine subspecies and two species of bristlecone pine) is one of the oldest pine groups in the United States. Fossil records date the group back at least 45 million years. It has a rich history of allopatric speciation, and though many theories exist explaining its precise evolutionary history, many questions remain. By understanding how and why a species has its current range and ecological characteristics, one can better understand the evolutionary history of the species. Secondly, this project is aimed at current policies involving resource management such as water storage and agricultural systems. Through analysis of the foxtail pine's tree-ring record, it is shown that growth patterns significantly deviate on scales of at least 30 years. Since the foxtail pine is most sensitive to temperature, this indicates that temperature patterns vary on scales of at least 30 years. If we were to experience 30-year trends of higher or lower temperatures than current "averages", many snowpack-dependent water storage systems and temperature sensitive crops could experience dramatic shifts in production. Thus it is hoped that all policies in this area would begin to take into account past climatic conditions and the likelihood that they will reoccur. Finally, in a broad sense, this project contributes to a better understanding of the Sierra Nevada. The subalpine ecosystem is one of the most sensitive and little understood systems in the Sierras. The scientific and photographic data gathered for this study help to fill the gaps in our understanding of the subalpine system. It is only through a better understanding of the system, that proper management can occur.

The natural world, and all its intricacies, has always fascinated me. I was born in a rural setting (Sequim, WA), but grew up in an urban setting (Chicago, IL). When I first moved to California in 1995 it was to San Diego. In my efforts to escape the urban sprawl in mid-summer heat, I discovered the East Sierras. Upon my first visit, I immediately felt at home. I was determined to return and live there someday, but filed it away as a dream. After starting in ESSP, I began learning under Dr. Robert Curry, who reawakened that dream of the East Sierras. When he mentioned a little known tree species of the Southern and Eastern Sierra timberline country and said that there's a capstone to be made out of it, I jumped for it. At times the project seemed like a goose chase, trying to find information on such an obscure tree, but the beauty of the landscape always reeled me back in. Going into the project I assumed that no one would know or care about the questions I was trying to answer about the foxtail pine. I soon found out how wrong I was. There is an entire community of scientists and laypeople in the East Sierras, who are interested in and practice the type of integrated science and policy work that ESSP is steeped in. It was in that community of learners and teachers that I found my niche and hope to continue to work with throughout my post-ESSP career.

I would like the capstone project that follows this letter to be assessed in the following areas:

- Application and Knowledge in the Physical and/or Life Sciences (MLO #3)
- Acquisition, Display, and Analysis of Quantitative Data (MLO #5)

For my study, I obtained all published work on the foxtail pine, as well as relevant work with other tree species. In addition, I researched the history of my study sites and the fields of dendrochronology and dedroclimatology. All of this information is integrated and evaluated in the introduction, discussion, and appendix sections of this study. New questions and future work are addressed in the discussion and future work sections of my paper. These items all fit under the description of MLO #3. The field visits, tree-ring database acquisition and analysis, and my GIS maps of the foxtail's range all fall under MLO #5. These issues can are dealt with in all sections of the capstone report.

The work done through the course of my capstone study has been a fantastic experience. I have gained a greater understanding about the logistics of fieldwork and evaluation of study methods. Through this project I have also made many professional contacts that will be invaluable for later work. It is my profound hope that this study will enrich others' understanding of the foxtail pine and South Sierra subalpine ecosystems even half as much as it has enriched my own. I feel that the skills and experience I gained in completing an ESSP capstone will help me transition smoothly into graduate studies and the professional world of science.

Sincerely,

Michael Bogan

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Abstract. The foxtail pine of the Southern Sierra (*Pinus balfouriana* ssp. *austrina* Grev & Balf) is a relatively unstudied timberline pine species. It inhabits the high country of the Sierra Nevada between the 37th and 36th parallels between 2700 and 3550 m, and often is the sole tree of the subalpine ecosystem. In this project, three sites on the margin and one site in the center of the foxtail pine's distribution were examined to identify how the tree's ecological characteristics change over its range. In addition, a raw ring-width database for three sites was analyzed to obtain a foxtail pine ring-growth index for the last 1000 years. From field visits it appears that the western and eastern margins of distribution are altitude limited, while the northern and southern limits may be due to ecological displacement from other timberline tree species: by limber pine (*P. flexilis*) in the south and by whitebark pine (*P. albicaulis*) in the north. Common ecological characteristics across the tree's range were the dominant granitic substrate, the omnipresent chinquapin (*Chrysolepis sempervirens*) understory shrub, and sightings of Clark's Nutcrackers (*Nucifraga columbiana*). Foxtail pine growth is temperature sensitive, so paleoclimatic data can be inferred from a tree-ring index analysis. From this study's analysis, it was inferred that significant climatic departures of at least a 30-year length have occurred in the last 500 years. Interpolation of paleo-climatic data should be used to inform current climate and resource management policies, given that many current policies are only adequate to compensate for trends far shorter than 30 years. Further studies of the foxtail pine are necessary so that a greater understanding of its sensitivity to climate change and clues to its evolutionary history can be obtained.

Introduction

Species Characteristics

Life at timberline in the Sierra Nevada is extremely harsh, and very few plants are able to survive in this limiting ecosystem. One of the most able and enduring tree species of the timberline community is the foxtail pine (*Pinus balfouriana*). The foxtail pine, a California endemic, is found in two distinct, widely separated populations (See Figure 1). The northern subspecies *P. balfouriana balfouriana*, is found in the Klamath Mountains of Northern California up to the Oregon border. Nearly 500 km to the south is *P. balfouriana austrina* of the Southern High Sierras. This designation of subspecies status is relatively recent, having been made in 1980. This came following an extensive hybridization experiment and morphological study of the northern and southern populations, among other pines of the *Balfourianae* sub-group (Critchfield, 1977; Mastrogiuseppe and Mastrogiuseppe, 1980). These two studies have been the major published attempts to understand the biogeography of the species, and many questions about the foxtail pine remain unanswered (Lanner, 1999). In this study only the southern subspecies *austrina* will be examined.

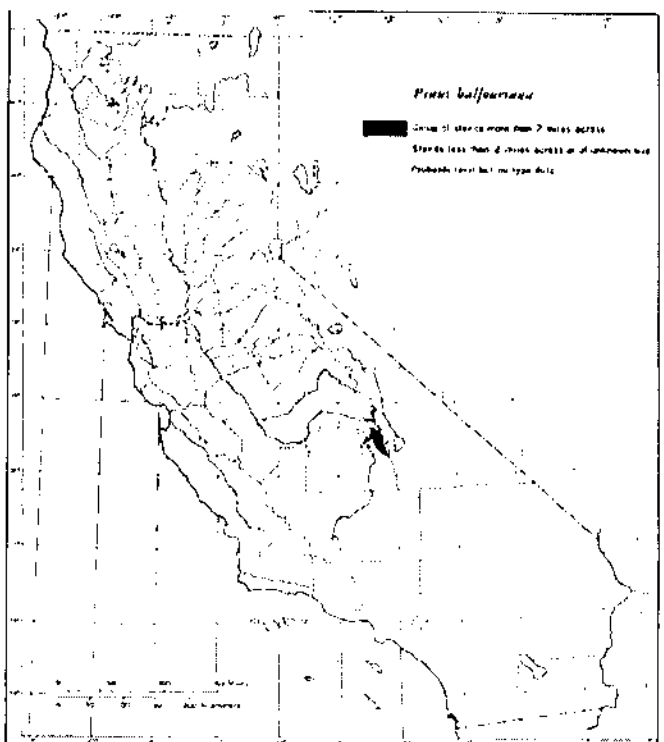


Figure 1: Distribution map from Griffin and Critchfield (1976).

The southern foxtail pine can be found roughly between the 37th and 36th parallels in the Sierra Nevada at altitudes ranging from 2700 m to 3700 m (Lanner, 1999). The trees are thought to thrive best on steep, south-facing slopes where very few understory plants or competing trees can grow. The largest known foxtail is located on the western edge of its distribution, above Timber Gap in Sequoia National Park (SNP), while the estimated oldest tree is on the south side of Split Mountain, at the very northern edge of its Sierran range (Arno, 1973). The southern foxtail can reach heights of 20 m and diameters of nearly 3 m. It almost always grows erect, unlike other timberline trees that often form *krummholz* or stunted, multi-trunked growth forms (Schoenherk, 1995). It is estimated that the foxtail pine can live up to 3300 years, but the oldest cross-referenced dating of tree rings have given ages of nearly 2000 years old (Sigg, 1983; Elliot-Fisk and Ryerson, 1987).

The foxtail is most commonly found on granitic substrates with very little geochemical soil development and relatively little groundcover. Each tree has a deep, spreading root system, much like a desert shrub, which may account for the low density in foxtail forests (Arno, 1973). It can be found in pure stands nearest to the timberline, but readily mixes with other conifers in the lower elevations of its distribution (Sigg, 1983). Due to the substrate and relatively low densities of foxtail trees, fire is not a common occurrence. Many charred stumps can be found throughout its distribution, but these are the result of single lighting strikes, which burn one tree at a time. Disease does not seem to be common at all, with most foxtails dying of 'old age' and the occasional lightning strike (Arno, 1973). Table 1 summarizes the basic life history characteristics of the southern foxtail.

Table 1: Southern Foxtail Characteristics

Elevational Distribution	2700-3700 m		*Substrate*	granitic, shallow soils
Maximum Height	~20 m		*Commonly Found*	SW-facing, steep slopes
Maximum Diameter	~3 m		*Forest Composition*	monotypic & mixed conifer
Maximum Age	known: ~2000 years probable: ~3300 years		*Seeds*	winged; also distributed by Clark's nutcracker
Needles	<4 cm long; remain up to 15 years; groups of 5		*Mean Temperature* *Mean Precipitation*	0°C to 12°C 30cm to 100cm

(From Arno, 1973; Mastrogiuseppe and Mastrogiuseppe, 1980; Sigg 1983; Schoenherk, 1995; Lanner, 1999)

Historical Distribution Questions

Paleontology

The foxtail pine's closest relative is the western bristlecone pine (*P. longaeva*). This species is distributed throughout the Great Basin on high, dry, and isolated ranges. It is also found in the White Mountains of California about 35km by air from the eastern-most Sierran foxtails. The two species are located within the same sub-group of pines, *Balfourianae* (Mastrogiuseppe and Mastrogiuseppe, 1980). It is thought that the foxtail is an offshoot of the bristlecone given that both share a common ancestor, the 44 million year old fossil *Pinus crossii* of Eastern Nevada (Critchfield, 1977). A descendent of *P. crossii*, the "proto-foxtail pine", likely underwent allopatric speciation after being separated into two populations by the subsidence of the Owens Valley and the uplift of the Sierra Nevada and White Mountains. This speciation event would have yielded our modern foxtail and bristlecone pines. The two species share many morphological traits, but are distinct enough in other traits to differentiate between the two. Most interesting in their relationship is the 100% crossability rate between the Sierran foxtails and the White Mountain bristlecones found by Critchfield (1977). Compare this with the 84% success rate between the northern and southern foxtails and you have an interesting story. It would suggest that the bristlecone and southern foxtail have shared genetic material more recently than the northern and southern foxtail groups have. Though its feasible that pollen could be blown on the prevailing westerlies from the Sierran foxtails to the White Mountain bristlecones, no natural hybrids exist according to Critchfield (1977).

Subspeciation of the northern and southern groups

How and when the foxtail pine came to be in its current disjunct distribution is a debated issue. The northern and southern subspecies, as mentioned previously, are separated by nearly 500 km. There is evidence that at one point in time foxtails were common between the current populations, as shown in fossil records from Lake County, CA. These records indicate that foxtails were present there in the late Pleistocene (probably Illinoian), more than 100 km away from the nearest modern-day foxtail and 1000 m lower in elevation (Critchfield, 1977). Most theories place the northern and southern subspecies as being separated for 2 to 3 million years, coincident with the uplift of the Sierra Nevada to its present height (Mirov, 1967; Bailey, 1970). However, efforts to hybridize the northern and southern subspecies have raised questions about the feasibility of the Sierra uplift timed theory. Critchfield (1977) found that northern and southern subspecies, when crossed, produce offspring 84% of the time. This figure, though lower than the expected 100% intra-subspecific success rate, is still relatively high. Critchfield (1977) goes on to postulate that perhaps the two subspecies have only been separated since the last few glacial advances, up to a hundred thousand years ago.

Questions are also raised in considering why the gap between the northern and southern subspecies is not smaller given the end of heavy glaciation events in the Central and Northern Sierras. Other species (whitebark pine, red fir, lodgepole pine, etc) recolonized the high country as the glaciers retreated, but foxtails appear to not have done so to the same degree. There is suitable habitat for the foxtail north of its present Sierran distribution, if considering elevation, slope, aspect, and precipitation, but none appear to be found north of the 37th parallel. Two theories for the lack of recolonization involve summer rainfall patterns and light intensity on differing slopes, however according to Schoenherk (1992), both theories have serious flaws and thus will not be considered here.

The story becomes more complex with the discovery in 1967 of a foxtail population on Sirretta Peak (Sigg, 1983). Sirretta Peak is 40 km south of the southern boundary of Sierran foxtail's distribution. It is a relatively low elevation site (2700-3050m) with a very diverse forest including red fir, white fir, Jeffery, western white and limber pines. With this discovery it became apparent that the Sierran foxtail can thrive at lower latitudes and perhaps with more competition than previously thought.

Genetic divergence among populations of a tree species whose distribution has been fragmented by climatic changes has been observed in many studies (e.g. Ledig et al, 1997). In 2000, the first genetic work on the foxtail pine was published, yielding many more hints about the species' past. Oline, Mitton, and Grant (2000) performed an allozyme survey of both the northern and southern subspecies of foxtail pines. They found that although the two groups are morphologically distinct, higher levels of differentiation were found among subgroups of each subspecies than between the two subspecies. The northern subspecies, *P. b. balfouriana*, especially showed this trend due to the varieties of soils on which it occurs (granite, serpentine and other metamorphics). They attributed this high variation to genetic drift and the mountain island effect, and hypothesized that differentiation had been occurring even before the northern and southern groups had been geographically isolated. If this is true, then it's quite probable that Sirretta Peak and Split Mountain, the extreme north and south outliers of the southern subspecies, show quite a bit of genetic differentiation.

A major goal of my capstone study is to provide an ecological baseline of data for the southern subspecies, from which appropriate study questions and sites can be determined for later genetic testing. According to Connie Millar (personal communication), a USFS forest geneticist, as important as genetic information is for understanding a species, it is not very useful without an ecological context. Thus, I hope this study can provide that context for later, more detailed studies of the southern foxtail pine.

Clues to the Past: the tree-ring record

The foxtail's amazing longevity and durability of its wood after death has allowed analyses to be made of changes in treeline and climate of the Sierra Nevada. Most notable have been Lisa Graumlich and Andrea Lloyd, whose work has analyzed changing timberlines and climate over the last 3000 years (Lloyd, 1997 & 1998; Lloyd and Graumlich, 1997). This work is done through the process of tree core extraction and analysis.

Trees form annual growth-rings inside their bark by division of the cambial cells, which produce large thin-walled xylem cells at the beginning of the growing season and thick-walled wood cells at the end of the growing season. This abrupt shift is easily seen, and can be used to delineate one year's growth from the next. A 5 mm wide corer can be used to extract a section of these rings from the base of the tree, and from the center to the bark you can count rings to determine the age of the tree. Often times one can make inferences about past climatic conditions at a site based on the relative width of these rings. Ring series from semi-arid sites, like those of the dry upper slopes that foxtails inhabit, provide the most reliable record of macroclimatic variation (Fritts, 1966). This field of study is known as dendroclimatology.

According to Fritts (1966), if ring chronologies are made from a number of trees in semi-arid sites with adequate corrections for trend and age, these chronologies can be used to construct an approximation of annual, or longer, climatic fluctuation. The longest climatic inferences have been made from the bristlecone pine, with a 5405-year record, but other pines are useful for constructing chronologies as well (LaMarche, 1974). Given the foxtail pine's spreading root system and drought-resistance, its tree-ring growth is most sensitive to temperature change, thus is useful for long-term temperature fluctuation analysis (Elliot-Fisk and Ryerson, 1987). This type of work is what Gramulich and Lloyd (1997, 1998) have done with the foxtail pine. Their time series show 3000 years of timberline fluctuations in response to macroclimatic changes, and hints at one of the most important uses that earth scientists can make of the foxtail pine.

Current Policy and Scientific Issues

Compared to other parts of the Sierra Nevada, the foxtail pine's distribution is relatively unaffected by human activity. Over 70% of its distribution is within Sequoia and Kings Canyon National Park, and a good deal outside of that is found in National Forest Wilderness Areas (SNEP Science Team, 1996). Given the difficulty in accessing most foxtail stands, they usually fall outside the range of human impact.

Foxtail pines are currently of great interest to earth scientists because of the clues they yield to past climatic conditions at timberline locations. I feel it is important to have a greater understanding of the foxtail's distribution so that we can better understand prior and potential future climatic conditions. A better understanding is also needed to estimate what effects human-induced global warming could have on this timberline species. Given that the foxtail and other timberline species occupy such a narrow range, I would suspect they are extremely sensitive to climatic shifts. Our present, possible elevated rate of climate change may be detrimental to many timberline species (Arno, 1993).

The foxtail pine is also included in the multi-agency, integrated study, the Sierra Nevada Ecosystem Project (SNEP). The project aims to identify and quantify the conditions of all Sierra Nevada ecosystems. The foxtail pine is currently seen as a 'stable' species, but it is noted that that could rapidly change with any change in management due to the foxtail's narrow distribution (SNEP Science Team, 1996). According to Millar (personal communication), understanding the historical variability of a species is essential for land managers interested in preservation.

The main goals of this project are to better understand how the foxtail pine's ecological characteristics change over its distribution and to use the tree-ring record to both examine for cohesive growth patterns across the foxtail's range and to understand implications for long-term climatic trends based on those tree-rings. These goals will be accomplished through creating a modern distribution map, making field visits of sites throughout the foxtail's range, tree-ring core sampling, and analyzing available tree-ring databases for the foxtail pine. I expect to find that competition is more intense in the margins of the foxtail pine's range. I also expect to find that the tree-ring record will illustrate climatic variation on far greater scales than are planned for with current resource policies, given that current policies are based on the last 30 to 70 years of climate data. This small time frame will most likely not represent long-term cycles or fluctuations that do occur with climate.

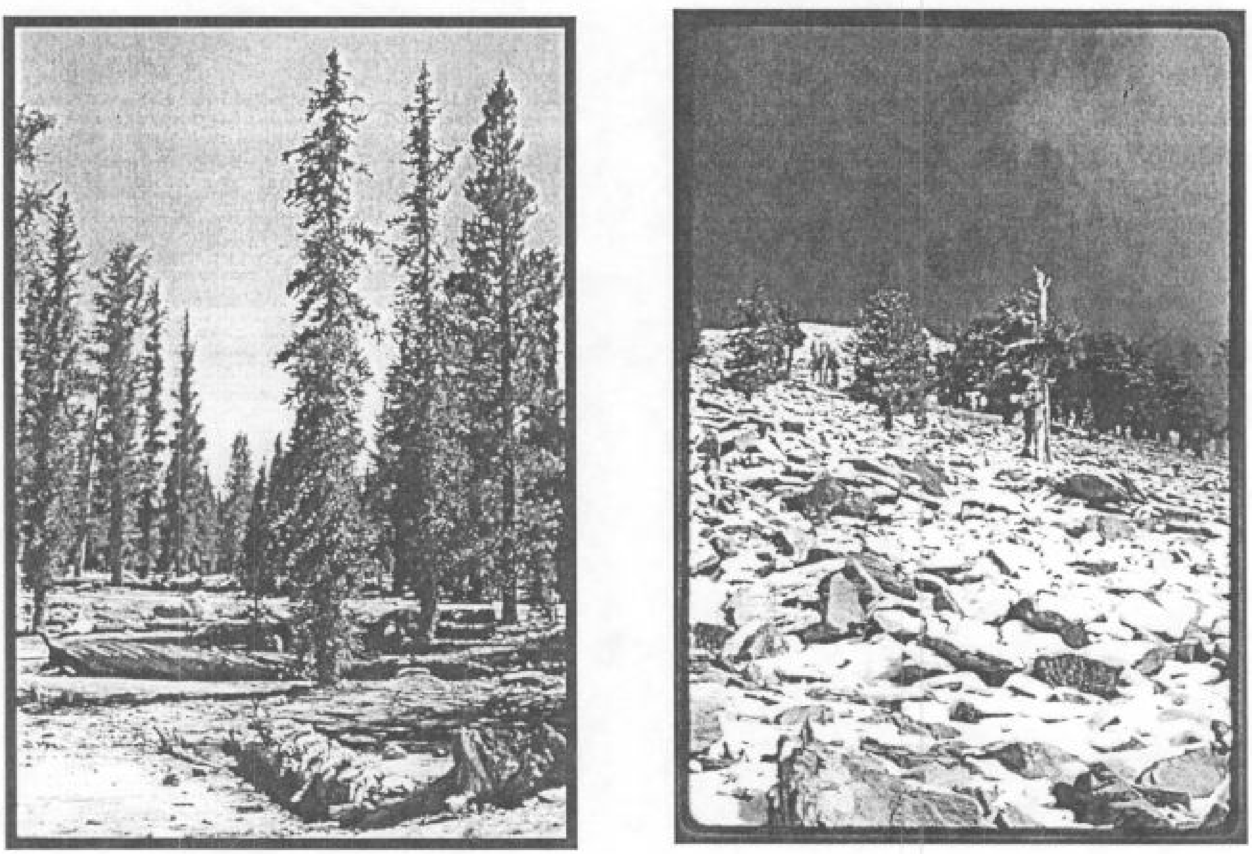


Figure 2: A flat, sheltered foxtail stand near Trail Peak (left), and a steep, windswept stand above Timber Gap (right).

Methods

GIS Distribution Map

Griffin and Critchfield (1976) created a distribution map of the foxtail pine, along with other major forest trees of California. As part of this study, I decided to create a more modern version of that map using GIS software. Using the GIS program *TNTmips*, I imported a 30-m resolution Digital Elevation Map (DEM) of California and Nevada, and extracted from that the area covering the foxtail's range. Then using data from Griffin and Critchfield, along with site data collected using topographic maps and a GeoExplorer II to collect GPS points, I created modern distribution map of the southern foxtail pine. From that map, the approximate area of the foxtail's southern range was calculated.

Field Observations

After analyzing available data on the southern foxtail's distribution, seven sites were chosen that best represented the variety of the range. Of those seven, four sites were chosen for detailed examination: Timber Gap, Sirretta Peak, Trail Peak, and Onion Valley. Each site, located within National Park or National Forest Wilderness areas, was accessed via hiking in and was visited for a few days to collect ecological information. Timber Gap is on the western edge of the foxtail's range, while Onion Valley is on the eastern edge. Sirretta Peak is the extreme southern outlier, and Trail Peak, while on the eastern edge, is connected to the vast central distribution of the foxtail centered around the headwaters of the Kern River.

Due to the number of unknowns about the foxtail forest ecosystem, these visits were made to gather preliminary ecological information, rather than scientific samples that address statistical questions such as age-structure of the forest and average density. For each field visit, species lists, general altitudinal distributions, forest characteristics, slope and aspects, and many photographs and sketches were made. Topographic maps were used to pinpoint microhabitats and at times a GeoExplorer was used to create vectors for GIS maps of the study sites. These data were then organized to form natural history accounts of each of the four study sites, which were compared and contrasted to look for ecological differences across the distribution. From these data, future and more stringent scientific sampling can be conducted at the four study sites.

Tree-ring Sampling, Data Acquisition, and Analysis

The tree-ring record is an extremely important set of data for earth scientists to utilize and understand, thus it is included under the scope of this study. Initially, I had planned to core a representative group of trees from each site to compare for differences in growth across the range, but soon realized that was not only an extraordinary undertaking due to the logistics of getting permits and performing the analyses, but also unnecessary. A NOAA database was located on the web with FTP-accessible files for tree-ring data at 3 out of the 4 sample locations I had chosen. So I decided to analyze those raw-data files and to collect a small field sample of cores to gain the experience of data collection first hand.

In field sampling, the cores were extracted from the trunk at breast height. The diameter at breast height (DBH) was measured, and then a manual increment-borer was drilled into the bark to remove a 5-mm wide radius of the trunk. Upon returning from the field, the cores were sanded and lightly polished to enhance their grain. The core was then examined with the Olympus VAS II, a dissecting microscope with a video monitor. The video controller and archiving program, run with the monitor, has an electronic measurement device that allowed individual ring-width measurements to be made. These yearly growth widths were then entered into Excel for de-trending and further analysis.

The main body of tree-ring data examined in this study came from NOAA's Paleoclimatic Data website. This 1987 database was collected by D.A. Graybill, Gary Funkhouser, and Rex Adams of the Laboratory for Tree-ring Research. These ASCII data files were imported from the website as text files, and opened in a word processor to remove unnecessary metadata. The files were then transferred to a spreadsheet and examined. The files contain raw yearly growth in units of 0.01mm for up to 30 trees at a given sample site. Trees generally show higher growth rates in youth and then decay to a relatively stable level afterwards. This trend was removed from the data by creating an expected growth for each decade based on a 100-year scaled mean, and then dividing the actual growth by the expected growth to obtain an index value (LaMarche, 1974).

Once the data was de-trended, comparisons were made between time spans within a site and comparisons in growth between sites can be drawn as well. For this, a Wilcoxon Rank-sum non-parametric test was run to detect statistically significant differences between time spans and between sites. In this manner, it is possible to examine for cohesiveness of climate response across the foxtail's range and for longer-term climatic trends that are reflected in all sites.

In addition to tree-ring analysis for the purpose of detecting possible climatic shifts, the NOAA database was examined for DBH versus age relationships. Planned future studies involving the foxtail pine include examining the age structure of foxtail forests across its range, so a simple method of determining age via field measurements is required. To create this method, a regression equation was calculated for each site using the age of the tree and an approximate DBH (2x total growth, since the rings represent a radius of the trunk). In this manner, age classes can be approximated based on easily taken DBH measurements in future sampling.

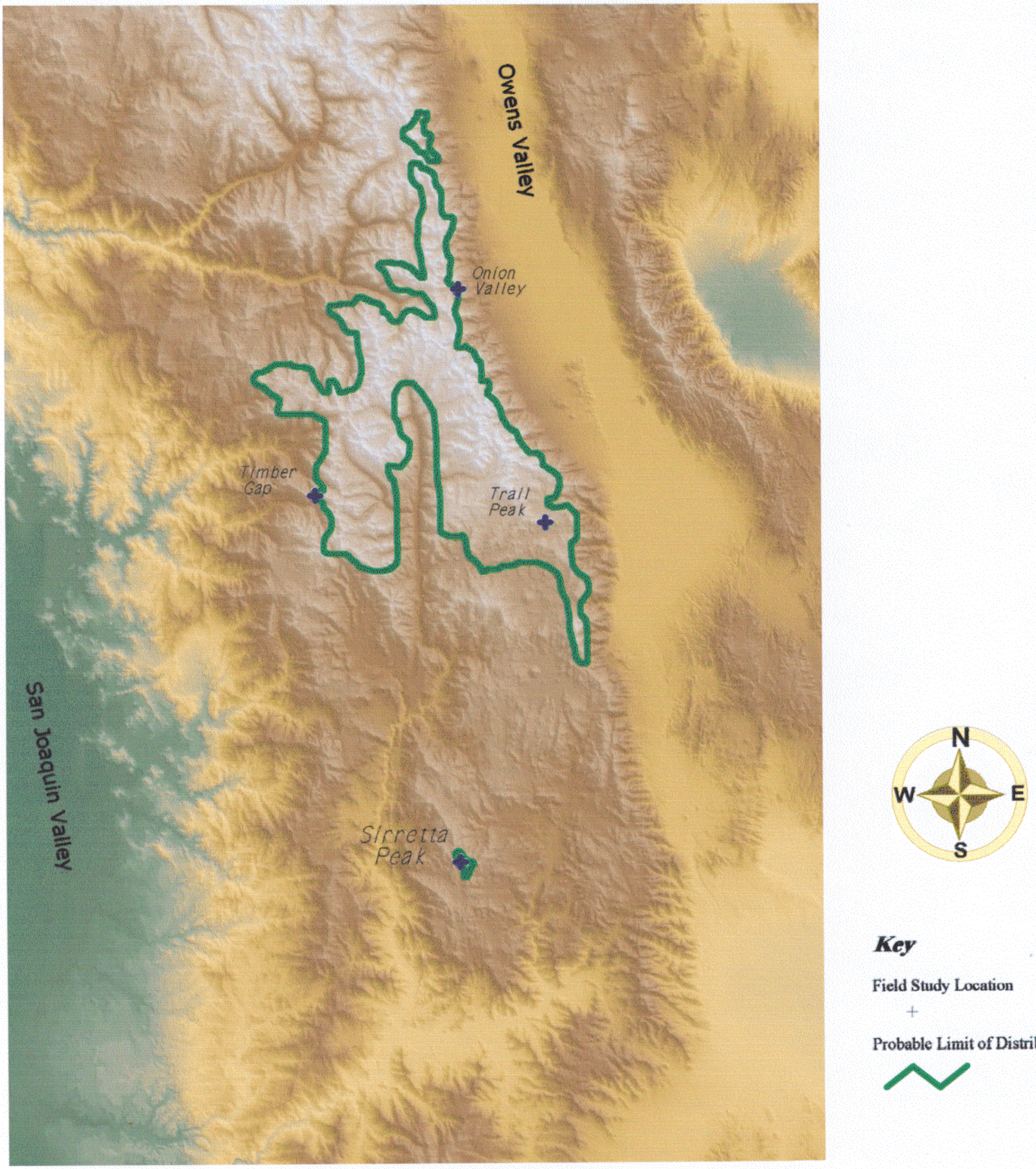
Results

GIS Distribution Map

The finished GIS product can be found on the page 13, immediately following this one. According to the spatial analyst tool in *TNTmips*, the total area enclosed by the polygon for possible foxtail pine distribution in the southern Sierras is 1465 km^2. From this range, those areas of an elevation between 2643 and 3534 meters were extracted for analysis. The elevation values were selected from the lowest and highest foxtail pines found in study site visits. The area between these elevations inside the possible range polygon was 924 km^2. This accounts mainly for elevational limitations on the foxtail pine and does not include possible range restrictions due to slope or aspect. For the scope of this study, though, the effective range of the Sierran foxtail pine is 924 km^2.

Southern Foxtail Pine Distribution

(DRAFT) MB



Key

Field Study Location

Probable Limit of Distribution

0 10 20 30 40 kilometers

Study Sites and Field Observations

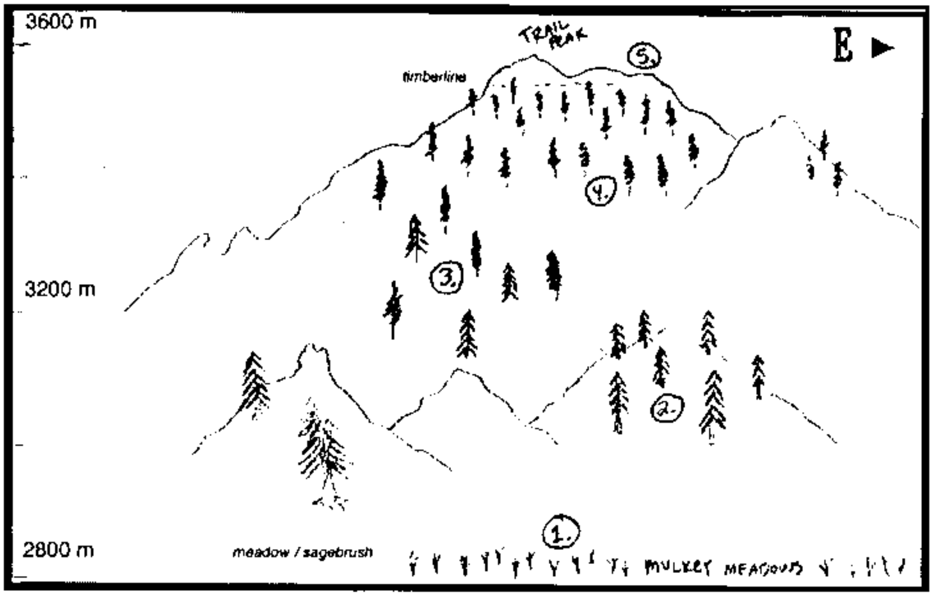
Trail Peak:

Though Trail Peak is on the eastern edge of the foxtail's range, it is connected to the center of distribution around the headwaters of the Kern River, and as such is the most 'typical' of foxtail forest types according to tree manuals and trail guides (see Schoenherk, 1992; Lanner, 1999). The forests here are wide open and often monotypic, consisting of mainly lodgepole and foxtail pines, and at times exclusively one or the other (Rourke, 1988). This is foxtail pine forest also sees quite a bit of human use with the Pacific Crest Trail and several golden trout-stocked lakes and streams nearby. It was surveyed on 6/3/00 and from 7/30-8/1/00.

Table 2: Site Characteristics at Trail Peak

Location	36°25'37" N 118°10'30" W
Site Elevation	2853 m to 3544 m
Foxtail Range	2927 m to 3534 m
Slope	3° in meadows to 45° on Trail Peak
Average Aspect	180°
DBH Values	5 cm to 1.5 m
Substrate	granite: deep soils in meadows to bare rock on peak

Near the trailhead to Trail Peak at Horseshoe Meadows, one can find many stumps of foxtail pines, remnants of the brief logging period in the 19th century. The study site Trail Peak is about 3 km from this area of logging. The site encompasses the area around Trail Peak, focusing on its south-facing flank. The geologic substrate of the site is granite. Areas of volcanic intrusions are nearby (Templeton Mountain, etc.), but no volcanics are present in the study area. The soils of the area range from the deep wetland soils of Mulkey Creek Meadows to moderately developed granitic soils on the talus of Trail Peak to pure granite boulders with almost no soil on the steep slopes of Trail Peak. The main vegetative communities here are meadow, sage scrub, mixed forest (foxtail and lodgepole), pure foxtail forest, and alpine fell field (*See Figure 3*).



1. Meadow / sage scrub
2. Lodgepole forest
3. Lodgepole / Foxtail mix
4. Pure Foxtail
5. Alpine Fell-Field

(Aspect: 180°)

Figure 3: Field sketch of elevation gradient at Trail Peak

The main understory plant of the foxtail forest here is the bush chinquapin (*Chrysolepis sempervirens*), making up around 10% of the ground cover. The other 90% consist of a combination of exposed granite boulders and soils with fallen needle, branch and cone litter. Though the entire study site has quite a variety of species (*See Table 3*), the pure foxtail forest is quite limited in floristic components. Individual trees are fairly uniformly spaced (5-10 m apart) and reach maximum heights of around 18 m. It seemed that recruitment was ample over the site, with 0.5 to 1 m saplings found at all elevations around Trail Peak.

Three nesting pairs of Clark's Nutcrackers (*Nucifraga columbiana*) and several fledglings were also seen in the border of the mixed and pure foxtail forests. This species is a keystone species for the ecosystem due to its habit of breaking open pinecones and spreading seeds through the forest (Lanner, 1996).

Table 3: Observed Species List for Trail Peak

Trees	Shrubs	Birds	Mammals	Flowering Forbs
Cerocarpus ledifolius [3]	*Arctostaphylos nevadensis* [3]	*Cathartes aura* [4]	*Canis latrans* [4]	*Aquilegia truncata* [4]
Juniperus occidentalis [4]	*Artemesia tridentata* [1]	*Falco sparverius* [4]	*Eutamis alpinus* [1]	*Castilleia lemmonii* [1]
Pinus balfouriana [1]	*Chrysolepis sempervirens* [1]	*Nucifraga columbiana* [1]		*Erigonum ovalifolium* [1]
P. contorta [1]	*Ribes sp.* [1]	*Poecile gambeli* [4]		*Epilobium sp.* [2]
Salix sp. [2]		*Salpinctes obsoletus* [1]		*Erysimum pereme* [1]
		Sitta canadensis [1]		*Heracleum lanatum* [1]
		Sphyrapicus thyroides [4]		*Lupinus sp.* [1]
				Monardella odoratissima [3]
				Ranunculus eschscholtzii [2]
				Sphenosciadium capitellatum [2]

Note: 1. Common 2. Limited habitat 3. Rarely seen 4. Single sighting

About 10 m below the summit on the south slope of Trail Peak is where the highest-elevation foxtail pines are found. The timberline was approximately 50 m lower on the less steep north-facing side of the mountain (*See Figure 4a*). This gently sloping northern exposure was home to the alpine fell-field vegetative community, as well as remnant wood from foxtails that had once occupied this area above the modern timberline (*See Figure 4b*). These altithermal remnants represent movement into higher elevations in times of more favorable climatic conditions (Curry, personal communication). Recruitment was occurring at all aspects directly below timberline, indicating that the current timberline is relatively stable.

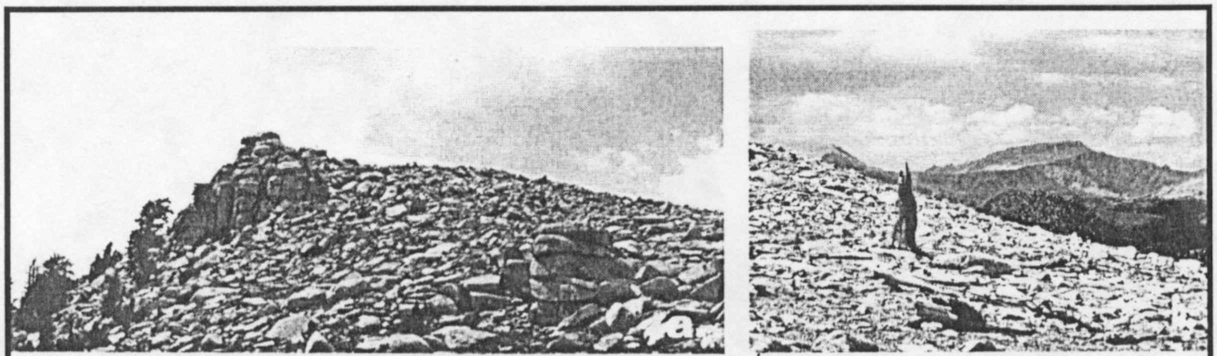


Figure 4: a. Trail Peak, to the left is south; b. altithermal remnant on north slope of peak.

Onion Valley:

The Onion Valley sample site encompasses a semi circle of peaks and slopes facing southeast towards the Owens Valley. It is located on the east edge of the foxtail's range, and also along the northern boundary. Split Mountain, 24 km to the north, is the extreme northern outlier for the southern foxtails, but was not included in this study due to time limitations and difficulty of access. Therefore the Onion Valley site is serving as representative of the foxtail at the northeast corner of its range. It was visited from 7/13-7/14/00 and on 7/19/2000.

Table 4: Site Characteristics from Onion Valley

Location	36°46'26" N 118°19'55" W
Site Elevation	2800 m to 3800 m
Foxtail Range	2800 m to 3380 m
Slope	0° in meadows/lakes to 80° on University Peak
Average Aspect	120°
DBH Values	4 cm to 2.5 m
Substrate	granite: soils deep in meadows/lakes with bare rock on talus/peaks

The substrate here and elsewhere in the study site is mainly granite boulders and talus slopes, with some lightly developed granitic soils. The most well developed soils are in the areas surrounding the glacial lakes and meadows of the basin, neither of which are commonly home to foxtail pines. In the northwest corner of Onion Valley is Kearsage Peak, a metamorphic peak, but it is not included in the study area. Ecologically, the area is much more diverse than the Trail Peak study area. The most common vegetative communities were meadow, riparian forest, mixed forest, foxtail/whitebark forest, pure foxtail forest, *krummholz* whitebark forest, active scree slope, and alpine fell-field. Also, unlike the Trail Peak area, a tree species (whitebark pine) at Onion Valley existed at a higher elevation than the foxtail, suggesting competition issues in this area of the foxtail's range (*See Figure 5*).

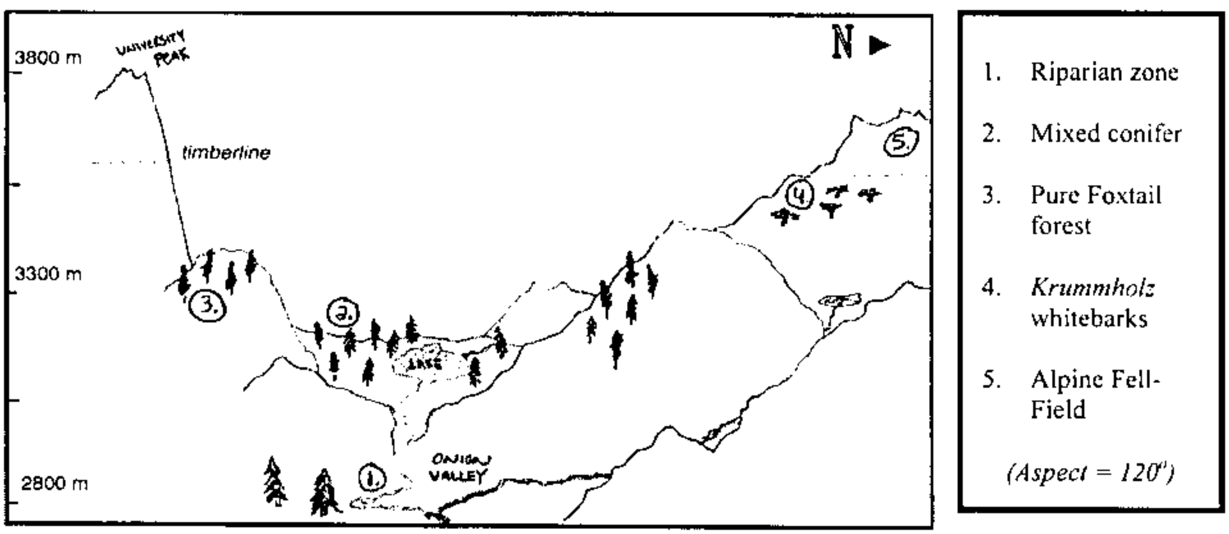


Figure 5: Field sketch of elevation gradient at Onion Valley

With ten species of trees found here, the ecosystem dynamics are far more mosaic-like than in the Trail Peak area. The dominant ground cover depends largely on what microhabitat is being examining. In the meadows and riparian areas, the ground cover is nearly 100% perennial and annual grasses and flowers, while in the drier mixed forest chinquapin (*Chrysolepis sempervirens*) and manzanita (*Arctostaphylos nevadensis*) are also present, with up to 30% bare rock and soil. Great Basin shrub species such as the big sagebrush (*Artemesia tridentata*) and buckwheat (*Erigonum nudum*) are also present in these xeric forest areas. In the foxtail/whitebark, pure foxtail, and *krummholz* whitebark forests, the ground cover is about 15% chinquapin, with the remaining open ground being granitic substrate with needle, cone, and branch litter.

Table 5: Observed Species List for Onion Valley

Trees	Shrubs	Birds	Mammals	Flowering Forbs
Abies magnifica 1	*Arctostaphylos nevadensis* 1	*Cyanocitta stelleri* 3	*Citellus lateralis* 4	*Adenocaulon bicolor* 1
Cerocarpus ledifolius 1	*Artemesia tridentata* 1	*Nucifraga columbiana* 1	*Eutamis alpinus* 1	*Allium validum* 2
Cerocarpus montanus 3	*Chrysolepis sempervirens* 1	*Poecile gambeli* 3	*Odocoileus hemionus* 4	*Aquilegia truncata* 3
Pinus albicaulis 1	*Erigonum nudum* 1	*Selasphorus platycerus* 1		*Castilleia lemmonii* 1
P. balfouriana 1	*Ribes sp.* 1	*Tachycinta thalassina* 3		*Heracleum lanatum* 1
P. contorta 2				*Ivesia santolinoides* 1
P. jefferyi 3				*Lupinus sp.* 1
P. monticola 1				*Mimulus guttatus* 2
Populus tremuloides 2				*Monardella oderatissima* 1
Salix sp. 2				*Phylox sp.* 1
				Primula suffrutescens 2
				Sphenosciadium capitellatum 2
				Zauschneria californica 1

Note: 1. Common 2. Limited habitat 3. Rarely seen 4. Single sighting

At the time of visitation (mid-July), the foxtail pine was at the peak of its pollen and cone production. Nearly all foxtails observed had male cones that gave off yellow pollen at the slightest wind or touch (*See Figure 6*). This time period was the peak for such activity that was observed between June and October 2000. Foxtail recruitment was high in certain areas on Onion Valley, particularly at recent avalanche sites and areas of lesser slopes. All sizes of foxtails were found, as well as one tree near Gilbert Lake that is likely the largest foxtail in the East Sierras (close to 20m tall and 2.5m DBH). In all the population seemed very healthy and stable, though it faced heavy competition pressure at both its upper and lower elevational limits.

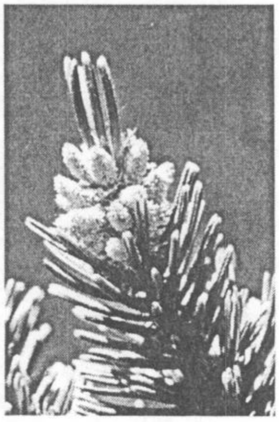


Figure 6: Male pollen cones at Onion Valley.

The Clark's Nutcracker was extremely prominent in Onion Valley, with many birds seen flying, and one observed taking seeds from a foxtail pinecone, while still on the tree. Three mating pairs of birds were seen as well as several fledglings. The abundance of trees there provided ample habitat for the seed-dependent bird.

Timber Gap:

Timber Gap is located in Sequoia National Park, on the western edge of the foxtail's range. West of there, the Sierras drop off to the foothills, and no suitable high country exists for alpine species. The site is within sight of the Central Valley, and on half of the observation days air quality at Timber Gap was reduced due to prevailing winds blowing smog up from the valley. Field observations were made later here than at the other sites (10/7-10/8/00 and 10/29/00), and the season's first snowfall occurred on the last visit.

Table 6: Site Characteristics at Timber Gap

Location	36°28'04" N 118°35'49" W
Site Elevation	2625 m to 3515 m
Foxtail Range	2988 m to 3365 m
Slope	2° at Timber Gap to 38° on Empire Peak
Average Aspect	195°
DBH Values	2 cm to 2.7 m (largest in study)
Substrate	schist and marble near TG to quartz diorite on peak

Soils are well developed in the metamorphic saddle of Timber Gap, and nearly non-existent further up slope in the quartz diorite of Empire Peak. The metamorphic soils were home to quite large red firs and whitebark pines, but no foxtail pines. Upon reaching the metamorphic/quartz diorite contact zone, however, foxtails become the dominant tree. This may be the result of the geologic substrate's ability to form a soil, but could also be the result of an altitudinal gradient. The main vegetative communities of the study area are sage scrub, mixed forest, pure foxtail forest, and alpine fell-field (*see Figure 7*).

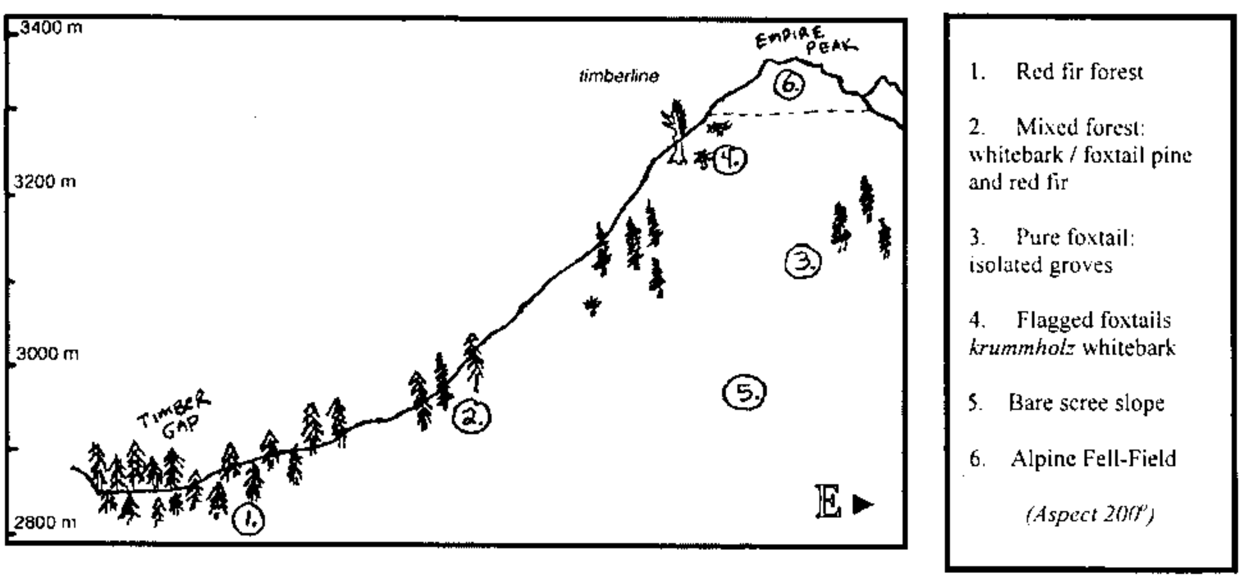


Figure 7: Field sketch of elevation gradient at Timber Gap.

The number of species observed here was much lower than at the other sites. Timber Gap was sampled the latest in the season, thus no wildflowers were identified. (*See Table 7*). The system here seemed limited by snowpack and climatic conditions as the dense red fir forests occurred only in protected areas with moderately developed soils, and the pure foxtail forests on the upper slopes were very discontinuous. Each sparse grove on the slope contained from 8 to about 50 trees, and the groves were distributed in a seemingly random manner across the slope. Some areas showed dense recruitment of 20 to 30 saplings, while others were limited to a group of 5 to 10 large old trees.

Table 7: Observed Species List for Timber Gap

Trees	**Shrubs**	**Birds**	**Mammals**	**Flowering Forbs**
Abies magnifica [1] *Pinus albicaulis* [1] *P. balfouriana* [1] *P. contorta* [3]	*Arctostaphylos nevadensis* [1] *Artemesia tridentata* [1] *Chrysolepis sempervirens* [1] *Ribes sp.* [1]	*Nucifraga columbiana* [1] *Poecile gambeli* [3] *Selasphorus platycerus* [1]	Eutamis alpinus [1]	(too late in season)
Note: 1. Common 2. Limited habitat 3. Rarely seen 4. Single sighting				

Like all other study sites, the dominant understory species at Timber Gap was chinquapin. In the dense red fir forests of the lower elevations, chinquapin and other understory plants are rare, with needle and branch litter being the dominant cover. Above 2990 m, the soil fades to bare marble and then quartz diorite and the chinquapin thrives with nearly 15% cover, both in exposed areas and under the canopy of foxtails (*See Figure 8b*). In the higher elevations of the site, the foxtail is the only upright tree, but the whitebark exists as a *krummholz* shrub and part of the foxtail forest understory above 3260m. One whitebark pine was found at 3400m, above the highest foxtail, but was a small 0.75m tall shrub. A large foxtail snag was also found above the current foxtail timberline (*See Figure 8a*).

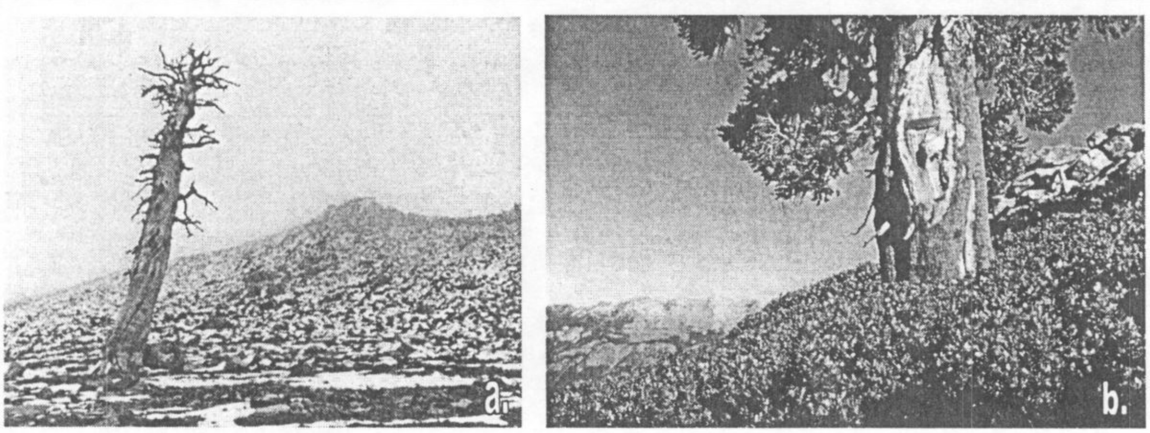


Figure 8: a.) A foxtail snag above current timberline; b.) a foxtail surrounded by chinquapin, looking north to Alta Peak.

One Clark's Nutcracker was seen and several were heard during the first field visit, but their activity seemed much less than earlier in the season, at the other sites. The second visit followed the season's first storm, and no sign of animal activity was observed.

Sirretta Peak:

The extreme southern outlier in the foxtail pine range is Sirretta Peak. It is 25 km south of the next nearest grove, and occupies a relatively low elevation. The site, located in Sequoia National Forest, was visited from 7/12-7/13/00. Though the area is dissected by an off-highway vehicle trail (OHV Trail 34E12), little evidence of human or vehicular impact was seen at the site.

Table 8: Site Characteristics at Sirretta Peak

Location	35°55'26" N 118°20'02" W
Site Elevation	2590 m to 3041 m
Foxtail Range	2643 m to 3039 m
Slope	3° at Sirretta Pass to 34° on peaks
Average Aspect	180°
DBH Values	3 cm to 1.5 m
Substrate	granodiorite: shallow soils, little exposed rock

As expected for a species at the extreme edge of its range, competition was high at Sirretta. More tree species were observed here than at any other location (*See Table 9*). Nearly the entire study area was mixed forest type, with a small stand of pure foxtails on the saddle of Sirretta Peak. Timberline is not reached at this low elevation, though there are areas of rock outcrops on the peak which support no trees. This site also was the only where limber pine (*Pinus flexilis*) was observed. This species occupies the foxtail's ecological niche in the ranges of Southern California and the several ranges of the Great Basin (Lanner, 1999). According to Griffin and Critchfield (1972), limber pine is also found at Onion Valley, but none were observed in this study. Due to the phenotypic similarities between limber pine and whitebark pine on the margins of their distribution, positive identification was made by examining individual tree cones.

Despite the heavy competition, foxtail recruitment was high at the site and the population appeared very stable. The pure foxtail stand on the saddle of Sirretta Peak had the highest density of standing dead foxtails. The saddle is an area about 300 meters long, in between the two granitic outcrops of Sirretta Peak. The area is extremely flat with slopes of 0° to 5°, and likely receives a deeper snowpack than the surrounding steep slopes. The cause of such a high density of dead trees on the saddle could not be determined through field observations.

Table 9: Observed Species List for Sirretta Peak

Trees	Shrubs	Birds	Mammals	Flowering Forbs
Abies concolor [1] *Abies magnifica* [1] *Cerocarpus ledifolius* [1] *Pinus albicaulis* [1] *P. balfouriana* [1] *P. contorta* [1] *P. flexilis* [1] *P. jefferyi* [1] *P. monticola* [1] *P. ponderosa* [4] *Salix sp.* [2]	*Arctostaphylos nevadensis* [1] *Artemesia tridentata* [1] *Chrysolepis sempervirens* [1] *Ribes sp.* [1]	*Cyanocitta stelleri* [1] *Nucifraga columbiana* [1] *Poecile gambeli* [1] *Selasphorus platycerus* [3] *Tachycinta thalassina* [1]	*Eutamis alpinus* [1] *Odocoileus hemionus* [4] (bats) [1]	*Arabis holboeii* [1] *Gilia aggregata* [1] *Lupinus sp* [1] *Mimulus sp.* [3] *Pentstemon newberryi* [1] *Pterospora andromedea* [2] *Sarcodes sanguinea* [2] *Zauschneria californica* [1]
Note: 1. Common 2. Limited habitat 3. Rarely seen 4. Single sighting				

The Sirretta population contains foxtails at lower elevations than all other sample sites. The first one was encountered on a southwest-facing slope on the trail up to Sirretta Pass. The common vegetative communities for the site were riparian, mixed forest without foxtails, mixed forest with foxtails, and pure foxtail forest (*See Figure 9*).

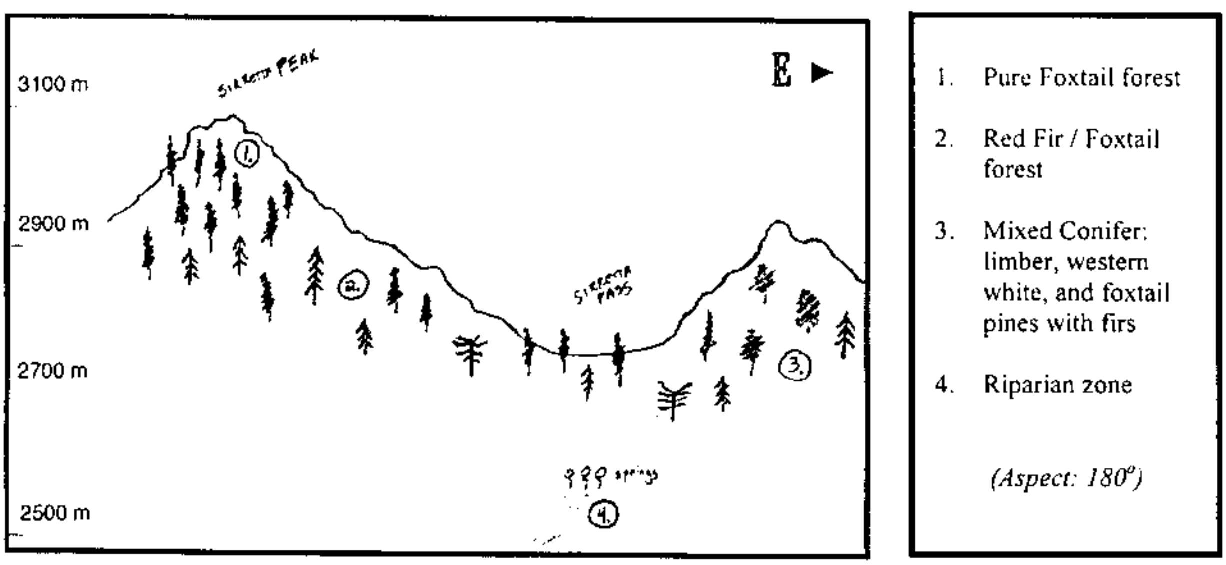


Figure 9: Field sketch of elevation gradient at Sirretta Peak.

The most common understory species here was once again chinquapin with manzanita a close second. The two combined provided nearly 40% of the ground cover of the area. Approximately another 5% was various annual flowers and grasses with the remaining area being granodiorite boulders and soils.

Several Clark's Nutcrackers were seen along with Steller's Jays, woodpeckers and various other lowland birds. Deer and coyote scat was found at Sirretta Pass, but no individuals were observed. The area was buzzing with insects, hummingbirds and butterflies and seemed to be emerging from winter quite energetically, as displayed by the snow plant and pine drops found here also.

NOTE:
For a site history of the four study sites see Appendix I.
For a page of thumbnails of photographs taken during field observations see Appendix II.

Tree-ring Analysis

Raw Ring-Width Data

The tree-ring database sampled represented a range of foxtail pines from 100 to 1050 years old. These data were from two locations at Timber Gap, TGL (n=18) and TGU (n=25), two locations at Onion Valley, ONV (n=21) and FLW (n=16), and one location near Trail Peak, CRQ (n=24). No tree-ring data was available from Sirretta Peak. These raw ring-widths were transformed into decadal mean widths, the results of which are shown in Figure 10 below. Due to the non-linear growth function that trees exhibit and the variety of ages sampled, it's clear that there is a tremendous amount of scatter among the sample groups. Some sites growth patterns appear to be nearly the inverse of other growth patterns, which may signal differing reactions to the same climate at various elevational levels. The lowest elevation sampled was at Onion Valley proper (2800m), and as seen in figure 1 this site deviates from the norm several times over the 1100-year record. An abnormal pattern is also seen with Cirque Peak (3300m), the highest elevation sampled, where restraints on growth (mean temperature, snow pack, etc.) are more extreme than other sites *(for a full-size color version of figure 10 see Appendix III)*.

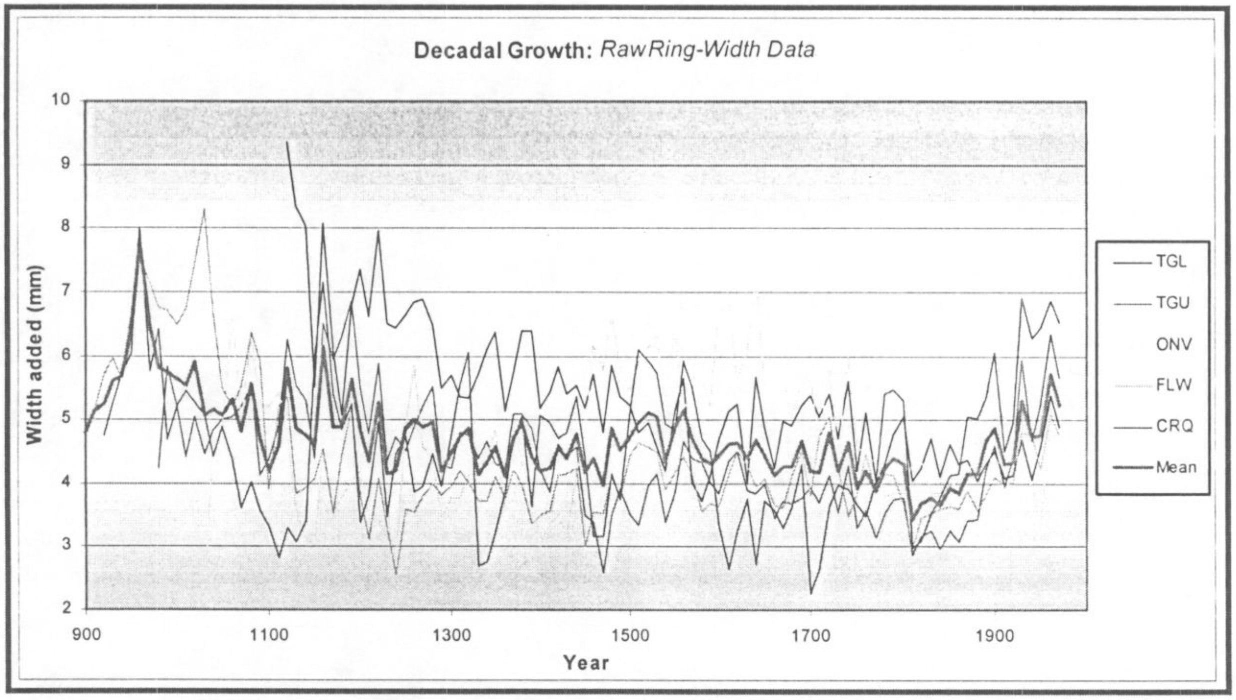


Figure 10: Raw ring-width decadal means and total mean for all sites.

Though not included in the statistical analysis of this study, the cores that were collected by the author were of great interest. Ten cores were collected from various sites in Inyo National Forest and analyzed in lab at CSU Monterey Bay. Though not cross-dated for accurate temporal placement, these cores showed trends similar to those seen in Figure 10 above, with varying periods of large ring-width growth and minute ring-width growth. See Figure 11 below for examples.

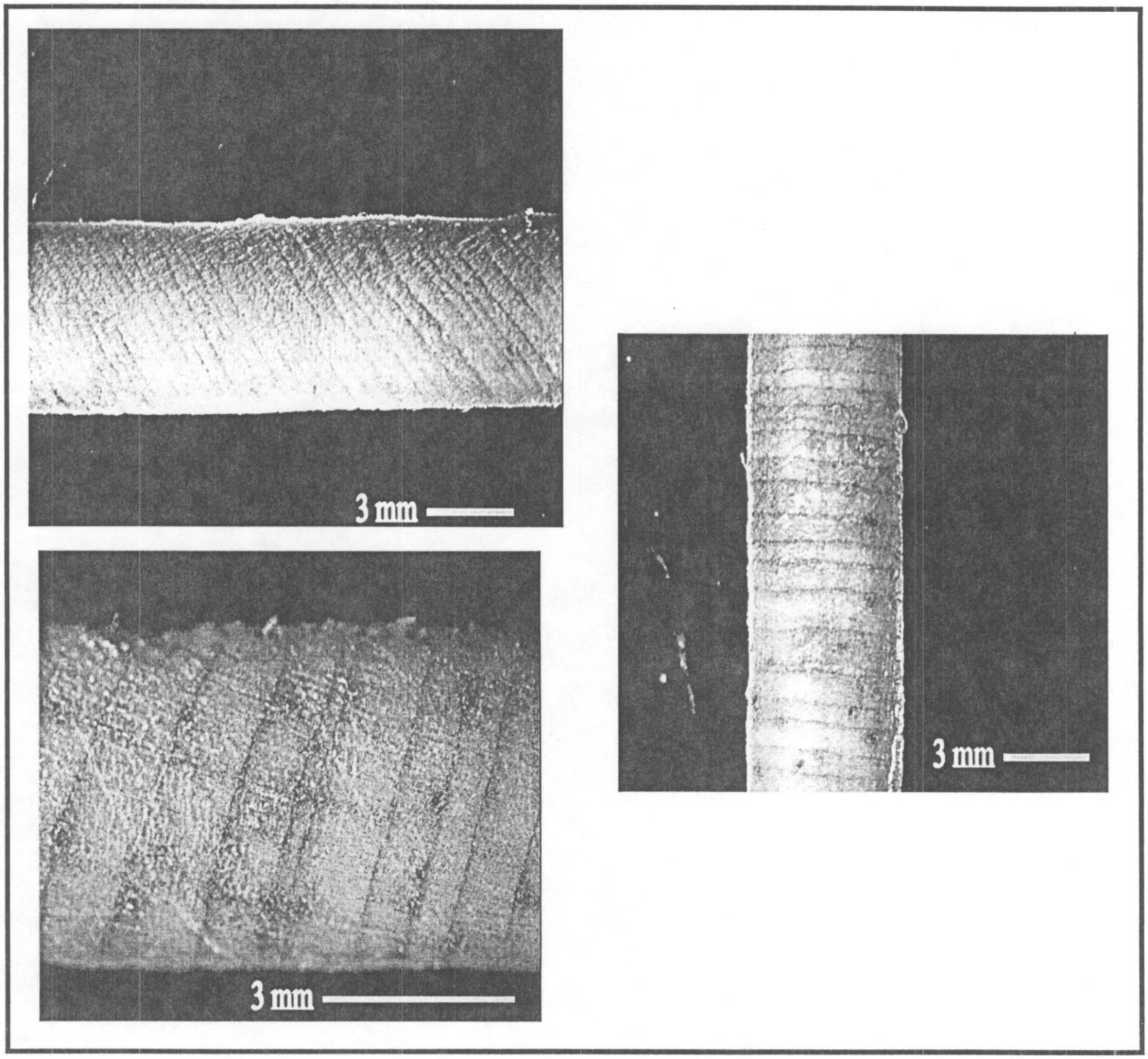


Figure 11: Foxtail pine tree-core images of varying scales collected and photographed by the author.

Growth Indices

The scatter of differing age classes and sample populations, as seen previously in Figure 10, is removed by computing a growth index value. All trees sampled (n=104) were individually treated to remove trends in growth over time in order to see how "normal" their growth was for any given period of time. Once tree-ring data is detrended, then analysis can begin for climatic variation. Figure 12 represents the detrended growth index for all samples over the foxtail's range (*for a full-size version of this graph see Appendix IV*). This removes most of the large spikes caused by young growth as seen in figure x above. A growth index value of "1" occurs when the observed tree-ring width is equivalent to the expected width given its decaying growth rate over time.

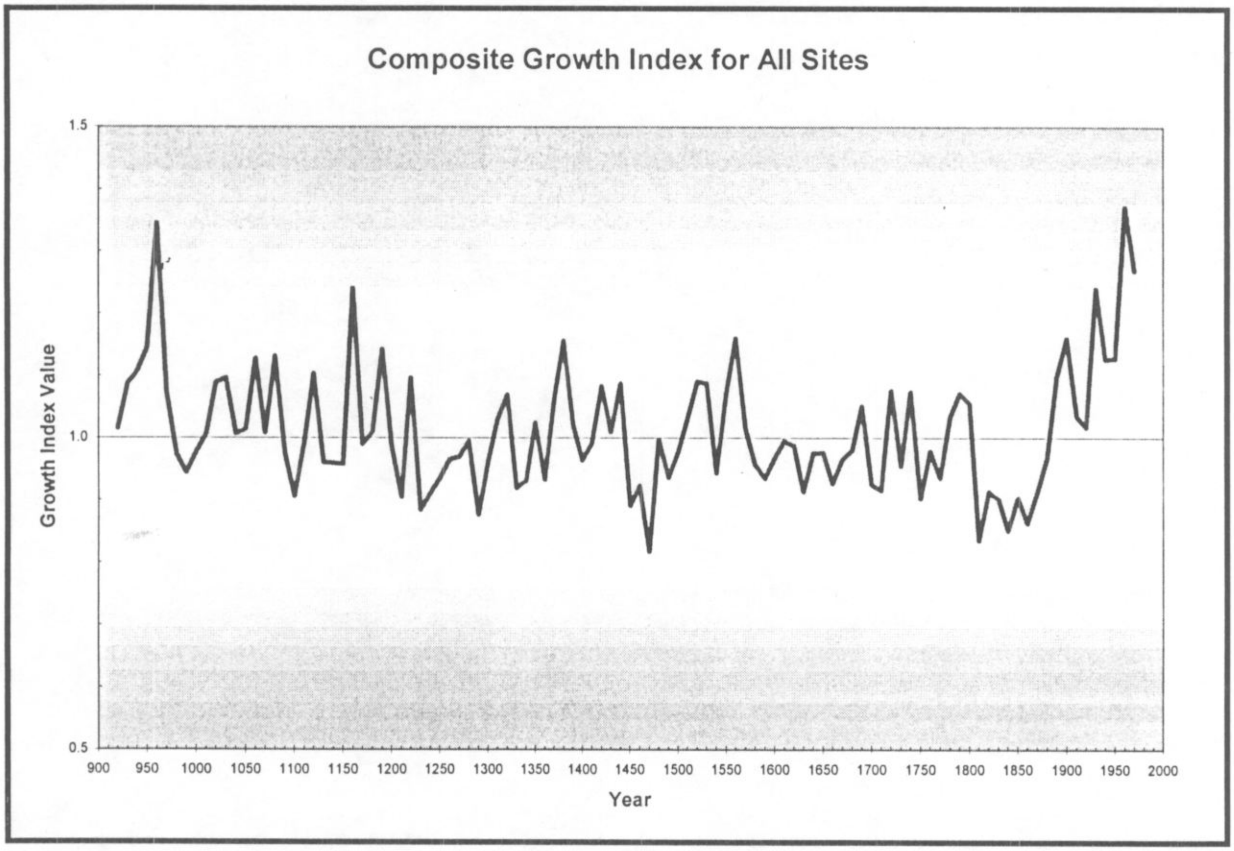


Figure 12: Graph of average decadal growth index for all sites (e.g. the data point '1970' represents the growth index for 1970-1979).

These data were then analyzed to look at statistically significant differences in growth between various time periods to illustrate some possible long-term climatic changes. The index graph shows dramatic decadal variation concerning the foxtail's growth response to environmental conditions. Since a single decade's variation could be attributed to an El Niño or similar effect, it is necessary to examine longer trends.

For this study, 30-year trends were examined to see if statistically significant variation in mean index values occurred on a greater than decade-long scale. I decided to use a thirty-year trend based on visual interpolation of the graphical results seen in Figure 12. I looked for trends that were obviously lower or higher than the standard index value (see the period from 1800 to 1870 for example), so that statistically significant differences were likely to be found. It is possible that significant variation on scales larger than 30 years exist in the data set, but these were not examined in this study.

Using a Wilcoxon rank-sum test, the thirty-year period of 1941-1970 was compared to the same length periods from 1441-1470 and 1811-1840. From the Wilcoxon Rank-sum test, it is clear that the 20th century period has a significantly higher growth index than both the 15th and 19th century periods ($n=104$; $\alpha=0.05$, $p<0.001$ for both). If the index value (which represents the growth's actual value relative to its expected value) is significantly higher for one time period than for another than factors controlling growth must significantly differ among these time periods as well. With a subalpine tree species, the primary factor controlling growth is climate. Thus, it can be inferred that the climate at the sample sites was significantly different among the 30-year periods examined by the test. This indicates that climatic stressors that affect the foxtail pine's growth may be occurring on time spans of at least 30 years.

DBH vs. Age Regression

Finally, the data was analyzed to create regression equations of diameter at breast height (DBH) versus Age. The equations and R^2 values are given in Table 10 below. The independent variable x represents a DBH value in meters, which is measured in the field. The dependent y-variable represents the approximate age of the sampled individual. All sites, with the exception of Onion Valley, had significant R^2 values and will be useful to further field sampling with the foxtail pine. The limitation of each equation is a DBH of around 10 cm. Onion Valley's low altitude and mesic environment may account for the lack of correlation between DBH and age.

Table 10: Regression analysis for calculating age from DBH at study locations.

Location	**Equation**	**R^2 value**	**Sample Size**
Timber Gap Lower	Y = 334Ln(x) + 795	0.77	N = 18
Timber Gap Upper	Y = 339Ln(x) + 899	0.79	N = 25
Timber Gap Combined	Y = 329Ln(x) + 851	0.74	N = 43
Onion Valley	Y = 36Ln(x) + 481	0.03	N = 21
Flower Lake *(in Onion Valley)*	Y = 363Ln(x) + 925	0.68	N = 16
Cirque Peak *(near Trail Peak)*	Y = 321Ln(x) + 824	0.77	N = 24

Discussion

Site Differences

Elevation and Competition

Though the foxtail's range is limited, there is quite a bit of ecological variation throughout its distribution. The two major limiting factors observed through field studies were site altitude and competition with other tree species.

In the central part of its range, represented in this study by Trail Peak, the foxtail pine is at its ecological optimum. The granite batholith of the Sierra reaches its greatest altitude, and the country is poor in soil and rich in granite boulders. This combination limits the ability of other species to encroach on the foxtail's dominance. At lower altitudes (>3100 m) and on the mesic edges of streams and meadows, the lodgepole pine is the dominant associate species. The lodgepole's wood and needles are not very durable however, so the foxtail's extremely dense wood and 20-year needle retention ability give it the edge. It is also in this central high country that the foxtail pine is of most importance to the subalpine ecosystem. Its seed provides forage to alpine chipmunks and habitat for many bird species. The slow decay of needle litter and snags add organic material to a very depauperate soil. Therefore, the importance of the foxtail pine to this subalpine system cannot be underestimated.

On the southern, eastern, and western edges of its range, the foxtail runs out of high country on which to grow. West of Timber Gap, the Sierras drop below 2800 m, on their slow descent to the floor of the Central Valley. On the way, the slope of the range decreases, and temperature and soil depth increase, giving the advantage to other tree species like red fir and Jeffery pine. The foxtail, with its xeric-adapted root system, cannot compete with these quick-growing, moisture-loving species, just as they cannot function in the foxtail's steep, windswept slopes. Thus, the foxtail's western limit is ecologically simple to understand, as the high country abruptly ends and there is a plethora of species against which the foxtail cannot compete.

In the south at Sirretta Peak, the foxtail encounters a suite of conifer species. It's incredible that the foxtail is found at all on Sirretta Peak. There are no high granite slopes, or rocky outcrops that the species normally thrives on. Instead, the mixed conifer forest there is the most diverse of all sites sampled. Most major Southern Sierra conifers are found there, in the rich alluvium of Big Meadow and Salmon Creek below Sirretta Peak, and at Sirretta Pass just east of the peak. The foxtail competes directly with Jeffery pine, and yet thrives (*See Figure 13*).

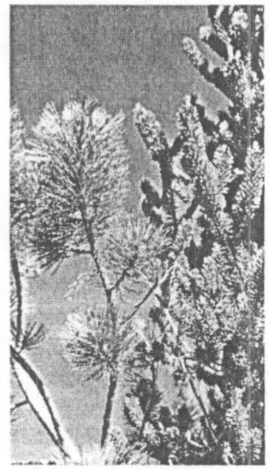


Figure 13: Jeffery (left) and foxtail (right) at Sirretta.

Most interesting of the foxtail's competitors at Sirretta Peak is the limber pine. This species is the timberline tree of Southern California's Transverse Ranges, and is also an associate of the bristlecone pine in many Great Basin ranges. The limber pine occupies the same niche as the foxtail, and at this point it becomes apparent that the foxtail does not have the same level of drought-adaptation that the limber pine does. On the saddle of Sirretta Peak itself, is a pure foxtail stand, while 300 m to the east is a parallel saddle about 40 m lower in altitude that is dominated by limber pines. Sirretta seems to the center of their interaction, as further south and east the foxtail yields to the limber pine, and further north in the Sierras the limber pine puts in only scattered appearances. Ryerson (cited in Rourke, 1988) found that in 43% of her sample locations along the margins of the foxtail's distribution, limber pine was an associate species. However Rourke (1988), in his sampling of the central high Sierras, found that lodgepole pine was by far the dominant associate species. These seemingly disparate observations help illustrate the interaction between the foxtail and limber pines. In the center of its distribution, the foxtail faces no competition for the timberline niche. On its margins, though, the limber pine is there to ecologically displace the foxtail pine from its niche. Given its far greater distribution, the limber pine must have adaptive traits more flexible (thus more genetically diverse or having a greater phenotypic plasticity) than those of the limited and specialized foxtail pine.

I had originally thought that the foxtail was moving south and colonizing the drier slopes of the Southern Sierra, based on the adaptations its root system have made. But to support that hypothesis, I also had to have a mechanism for dispersal. No foxtail groves are known to exist between Olancha Peak and Sirretta Peak, a 40 km distance. I thought it was possible that Clark's Nutcrackers had transported seeds from the main population south and accidentally founded a foxtail stand that then spread to cover the area adjacent to Sirretta Peak. However, according to Lanner (1996) the furthest Clark's Nutcrackers are known to fly in the Sierras is 7 miles (11.2 km), far shy of the distance needed. In addition, the foxtail pine's seeds are not a major part of the bird's diet, with other pines' larger seeds being more attractive. Thus there is neither a mechanism nor a real incentive for transport of foxtail seeds. It appears that the Sirretta stand of foxtails is a relict of a far wider distribution, perhaps from when climatic conditions were such that timberline was 300 to 400 meters lower than it is today. The question of why there are no foxtails between Sirretta and Olancha Peaks still remains unanswered though, as there are peaks with elevations similar to Sirretta in the interim distance. Further study is needed of that interim distance to gain insight on this edge of the foxtail's range.

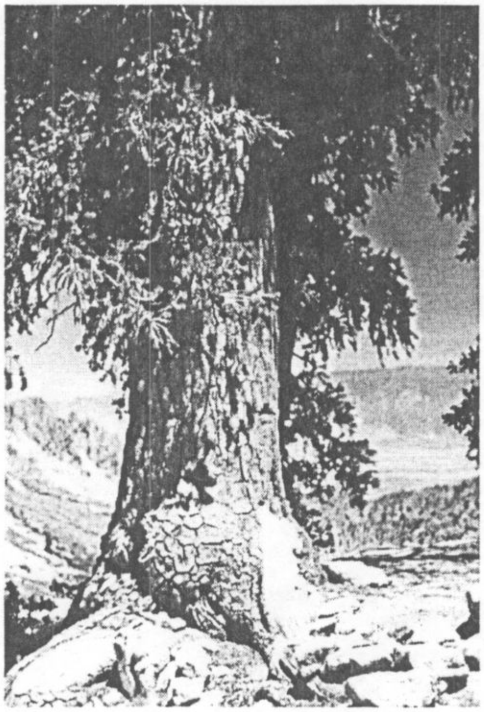


Figure 14: Looking east from Onion Valley.

Much like the western edge, the foxtail's eastern limitation can be easily described in one word: altitude. The fantastically steep scarp of the East Sierras clearly demarcates the edge of the foxtail's range. Many trees provide fantastic foregrounds to the backdrop of Owens Valley, and the 3000-meter elevation drop in 3 km of horizontal distance illustrates the abrupt end of distribution (*See Figure 14*).

The northern limit of the species is nearly as little understood as its southern limit. As mentioned earlier, there are no foxtails known north of the Split Peak area even though suitable habitat exists. The northern and southern foxtails presumably became separated by glaciation of the high Sierras, and underwent allopatric speciation after the split. Other conifers (e.g. whitebark and lodgepole pines), have since recolonized this intervening high country, but the foxtails have not. From observations at Timber Gap and Onion Valley, it is clear that *krummholz* whitebark pine can exist at higher altitudes than the foxtail pine. From this it can be inferred that in the colder, wetter Northern Sierras, the whitebark pine has a competitive advantage over the foxtail and thus preempts any possible northern migration of the Sierran foxtail. Also, the foxtail's xeric-adapted root system may now preclude it from moving back north into deeper snow packs and wetter soils. These are speculations, as no studies have been done on the interaction of foxtail and whitebark pines, but they are feasible explanatory mechanisms.

<u>Substrate</u>

Substrate may also play a role in determining the foxtail's range. Nearly all Sierran foxtails are found on granitic substrates. Of all field observations in this study, the only exception was at Timber Gap, where some trees are found on the metamorphic substrate below Empire Peak. The pure foxtail forest belt there is found on quartz diorite though, with red firs and whitebarks dominating on the schists and marbles of the Mineral King metamorphic belt.

North of Split Peak and south of Olancha Peak the metamorphics overlying the Sierran batholith and Tertiary volcanics are more common. The area of the central Sierras that the foxtails dominate is nearly all granite. Perhaps the slight advantage that the foxtail's adaptations lend on rocky, well-drained granitic substrates work against it on other substrates. Oline, Mitton, and Grant (2000) found evidence for allozyme differentiation between northern foxtails growing on serpentine substrates versus those on nonserpentine substrates. In some areas they found that northern foxtails were the only conifer that could grow on serpentine. This type of allelic sorting could be acting on the southern group as well, adapting them to the dominant substrate, granite, but not to other substrates. Fine-scale genetic testing of the Timber Gap group (like Rodgers, Millar, and Westfall's 1999 work with whitebark pines) could potentially answer this question, and is strongly suggested for inclusion in future studies.

Recruitment

At all study sites, substantial recruitment of foxtail pines was observed (*See Figure 15*). Timber Gap appeared to have the highest level of reproduction, with a lot of recruitment from a relatively small and sparse population, and displayed this trend all the way up to timberline, though *krummholz* whitebarks were found higher than sapling foxtails. Trail Peak showed recruitment up to and a few meters above the present timberline on the northeast-facing slope, with dense forests found throughout the site. Onion Valley, like Timber Gap, had heavy pockets of recruitment most prominently in recent avalanche areas. Surprisingly, given the heavy competition and lack of open areas, Sirretta Peak also had ample recruitment. It appears from observational data that the foxtail pine is stable in its present distribution, and may be moving slightly up-slope in areas.

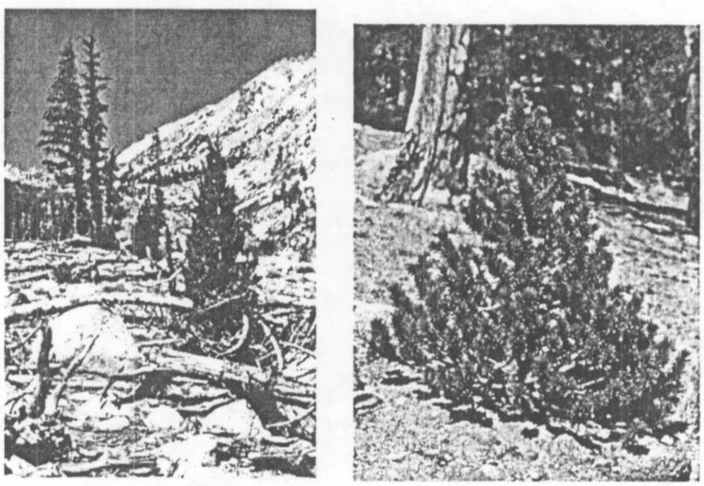


Figure 15: Recruitment at Onion Valley (left) and Trail Peak (right).

Tree-ring Data

Growth Index and Climate Change Implications

According to Eliot-Fisk and Ryerson (1987), the foxtail pine's tree record is useful for identifying climatic trends in temperature. With a longer growing season, comes a wider ring, while cool summers allow little new growth to be added. Using this information, it is possible to make inferences about past temperature regimes based on the growth index of a large enough sample of tree-cores. In this study, data from 104 tree-cores across the foxtail's range were analyzed to reduce the likelihood of skewed results based on localized events (e.g. avalanches). Though a much larger sample number and sample area is needed to make definitive statements about paleoclimatic regimes, much can be inferred from the data at present.

The growth index graph shows obvious variation in reaction to some stimuli, in this case presumed to be temperature. At times the data fluctuates wildly, but longer trends can be found in the scatter. A 30-year trend was chosen for examination because it is longer than current known phenomenon (e.g. El Niño / La Niña), and is a longer period of time than current policy is designed around. The middle 20th century was compared to two other 30-year periods and it was found that the growth indices do differ significantly between 30-year intervals. This implies that climatic conditions can operate on scales of thirty years or longer. Our current policies of water management operate with enough flexibility to deal with 6-8 year trends, but could not deal well with a 30-year drought or a 30-year change in snowpack dynamics due to sustained higher temperatures (Curry, personal communication). The tree-ring record shows that not only are 30-year or greater duration events possible, but that we may be in the middle of one right now with net positive precipitation and temperature departures (Curry, personal communication).

Other trees can give more detailed information, such as the bristlecone pine's 7500-year record of climatic inferences. However, Eliot-Fisk and Ryerson (1987) point out that at least 19 species in California are useful as indicators for past climatic conditions. The more species that are included in paleoclimatic analysis, the more detailed and accurate the picture of the past will be. Thus, the foxtail pine plays an integral part in the natural world's ability to assist humans to make wise policy decisions. If the tree-ring record of the bristlecone, foxtail, and other trees was understood 100 years ago, perhaps wiser planning could have been implemented for the management of natural resources like water. We need to recognize that our current infrastructure of dams, canals, and irrigated farms are not designed to meet a 30-year or greater magnitude climatic departure event. Hopefully, with continued growth in understanding the paleoecology and paleoclimatology of natural systems, we can reevaluate our current resource management strategies and plan not for the unrealistic "average" conditions, but rather for the reality of future climatic conditions.

Future Studies

The primary purpose of this study was to better understand the how the southern foxtail pine's ecological characteristics change over its range. The preliminary observations and analyses of the previous pages, will provide a base for more stringent scientific hypotheses and sampling. Though many details and conclusions arose from field observations in this study, even more questions were raised.

One direction of future study should be reexamination of the areas examined in this study, but using scientific sampling techniques to definitively identify range-scale differences in populations. Using the data in this study, one could determine proper sampling techniques to ascertain statistical differences in competition and recruitment between the four study areas. In addition, tree-core sampling is needed at the Sirretta Peak population. In this study, DBH versus age regression equations were created for Onion Valley, Timber Gap, and Cirque Peak, but not for the Sirretta Peak area. Thus, for sampling age structure at Sirretta a regression relationship needs to be established. It is the author's goal to carry out this work in conjunction with Mitch Lockhart, a fellow ESSP senior, over the course of this summer and fall.

A second area of future study should be genetic analysis. This method of study can be useful for seeing distributional patterns of genotypes that may not be evident through morphological examinations. Rehfeldt (1999) notes that genotypes are strongly influenced by climate and that tree species are comprised of populations with different climatic optima that have arisen through environmental selection operating on the system of genetic variability. He goes on to point out that in northern Idaho lodgepole pine populations only have to be separated by 200m of elevation to be sure of genetic differentiation. However, Rodgers, Millar and Westfall (1999) found little genotypic variation with elevation in a whitebark pine population, so differences are not always as pronounced as Rehfeldt found. Indeed, their study did not even find significant genetic variation between upright and *krummholz* forms of the whitebark, indicating a strong phenotypic plasticity in that species. Either way, genetic analysis of the southern foxtails could be useful in understanding how the species reacts to changes in geographic location, elevation, and substrate. Genetic analysis is also key to understanding how the Sirretta population fits into the historical range of the species. Connie Millar of the USFS has offered use of the PSW Forest Genetics lab in Albany, CA for the purpose of examining genetic variation in foxtails, and this will likely be the part of Mitch Lockhart's Capstone study as well.

Thus it is my hope that the present study and future studies planned for this summer and fall can contribute to the understanding of a little-known timberline species. With an elevated understanding of the foxtail pine, we can gain insight into the evolutionary history of the *Balfourianae* group of pines, the geomorphic history of the Sierra Nevada, and infer details about paleo-climates that would encourage reassessment of current policies on climate change.

Acknowledgements

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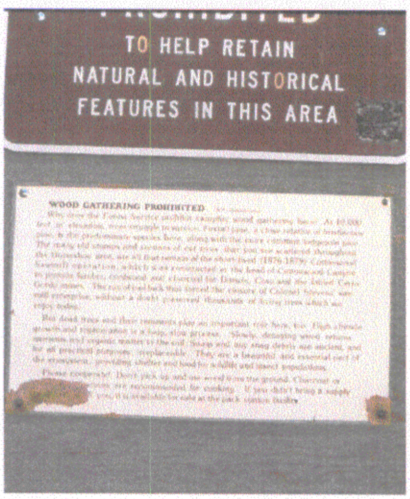
APPENDIX I

A History of the Four Study Areas

TRAIL PEAK

The foxtail pine is one of the few tree species in the Sierra Nevada that has not significantly been impacted by human activities such as logging and fire control. One major exception to this was a period of logging in the East Sierras during the 1870's. The Cerro Gordo mine, across Owens Valley from the Sierran foxtails near Trail Peak, had completely exhausted the timber supply of the Inyo/Coso Range and began to look to the Sierras. In 1873 a sawmill was built in Cottonwood Canyon, whose creek flows from the north slope of Trail Peak, and logging of lodgepole and foxtail pines began. Logs were sent down nearly 2500m to the Owens Valley floor, burned in charcoal kilns, brought by boat across Owens Lake, and then brought up 1200m to the Cerro Gordo smelters high in the Inyo Mountains. This extreme effort illustrates how desperate and greedy the mining corporations of the day were. By 1893, however, the mill was defunct following a bust at the mine. Though the mining lasted a short period, its effects are readily seen today in stumps and downed logs near Cottonwood Creek. Foxtail pines forests do not regenerate quickly and thus are very vulnerable to disturbance.



A Forest Service sign (left), and 130-year-old cut stump near the Cottonwood Creek trailhead (right).

The Forest Service has made the public aware of this history with a sign near the major trailheads of Horseshoe Meadows. In addition, there are strict regulations against the cutting or gathering of wood in many subalpine forests, including the one at Trail Peak, to which violators are subject to fines. The Trail Peak study site is also part of the Golden Trout Wilderness area, a 306,000 acre piece of land set designated in 1978 as part of the Wilderness Act. The area is protected from overuse by a trail permit and quota system, but is still open to pack trains. Every summer sees heavy visitation at the Cottonwood trailhead, with golden trout fishing and fantastic hiking drawing thousands of people in a few months.

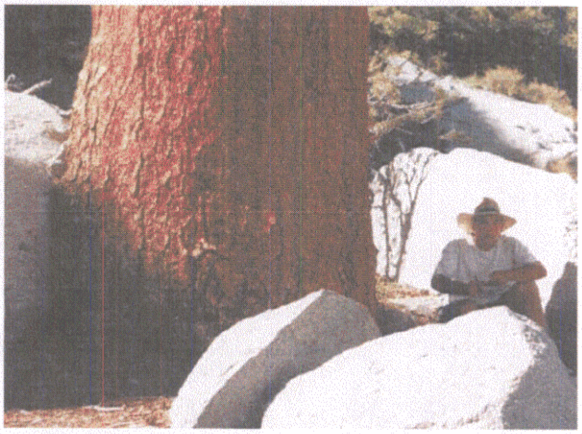
The greater Trail Peak/ Cottonwood Creek region is also home to the Foxtail Pine Research Natural Area. This 660-acre parcel of land is found in the Golden Trout Wilderness just east of Cottonwood Pass. The area carries few significant regulations apart from those of the wilderness area, with the only major distinction being that the area is limited to day-use only by foot traffic. It is a very representative foxtail stand, with a high proportion of mature trees. The Laboratory of Tree-Ring Research in Tucson has estimated some trees in the Research Area to be near 1500 years old.

The southern part of the Sierran foxtail's distribution was also heavily grazed in the late 1800's and early 1900's causing permanent meadow damage. Possible effects of this period on the immediately adjacent foxtail pine forests have not been studied. Much reduced intensity grazing continues today, but given the small number of cattle and their preference for meadows, foxtails are most likely not impacted. I have found no evidence of cattle presence in any foxtail pine forests as of yet, but they are present in Mulkey Meadows just below the foxtail pines of Trail Peak.

The deeply incised stream banks at Mulkey meadows (left), and ruins of the Cottonwood lumber mill (right).

ONION VALLEY

Onion Valley is located about 35 kilometers north of the Cottonwood / Trail Peak area. Like Cottonwood, Onion Valley is an extremely popular trailhead. From the parking lot, three main trails branch out, with all leading to destinations within the area, and one that leads over Kearsarge Pass into the western drainages of the Sierra. The Onion Valley region is also subject to a hiker permit and quota system and has developed quite a 'bear problem', with bear-resistant canisters a requirement for backcountry camping. Foxtail pines are found here at the Onion Valley campground near the parking lot. They are growing with quaking aspens, which is an unusual botanical cohort for the foxtail pine. The area is well watered by various tributaries of Independence Creek, and the foxtails do not reach their zenith until you reach the higher, dry slopes above the valley. Of interest to the foxtail connoisseur is the presence of some extremely large trees near Gilbert Lake above Onion Valley.



My colleague Mitch Lockhart seated next to the largest foxtail near Gilbert Lake, in Onion Valley.

Anglo-Americans first visited the area in the mid-1850's. By 1861 the area known as Gray's Meadow, a few miles east of Onion Meadow, sported a sawmill. As was common for the time, several locals spent time prospecting in the higher peaks above Gray's Meadow and Onion Valley. In 1864, a bit of silver was found in an outcrop on Kearsarge Peak, immediately north of the foxtails at Onion Valley. In what is now the trailhead parking lot of Onion Valley sprang the mining camp known as Kearsarge. The camp had a sawmill and an ore-processing mill. Many trees in the area were logged for the sawmill and mine shafts, but within a few years the meager vein wore out. In 1867 an enormous avalanche came off the side of Kearsarge Peak and wiped out the camp in Onion Valley, marking the end of the brief period of human impact.

No remnants of this period can be found today, with no stumps noticeable and the mineshafts marked only by *X*'s on the USGS topographic map. Today the area, in addition to the trailhead and campground, is home to a winter snow surveyors station and is quite popular for winter activities. Most of the area west of Onion Valley is protected within the John Muir Wilderness Area.

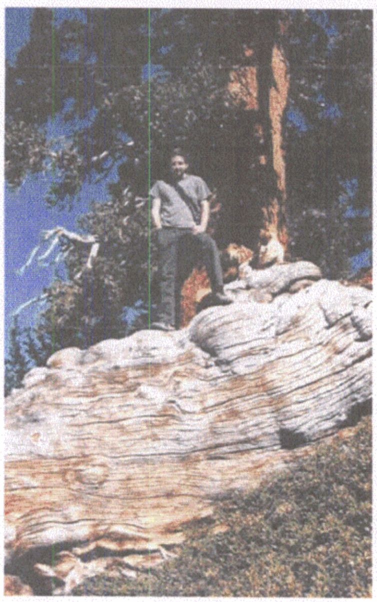
TIMBER GAP

The area encompassing the foxtail pines of Timber Gap is known as Mineral King. The main valley at Mineral King is located about 800 m below the foxtail pine covered slopes, and was first recognized by Anglo-Americans for its mineral wealth. Like Onion Valley, the valley was first scouted in the 1860's. In 1873 silver was discovered, and by 1879 a mining corporation had built the torturous road up the steep canyon into which Mineral King drains. The valley was quickly opened to logging, hydroelectric development and to the predecessors of today's tourists.

The dense red fir forest on Timber Gap was logged for firewood and mineshafts, and the Empire Mine opened just a hundred meters below the foxtail pines of Empire Peak's south slope. No record of foxtail pine logging exists, but surely it is possible given their proximity to the mining operations. Like the logging operations at Cottonwood and Onion Valley, operations ceased a short time later with the collapse of mining in the area.

In the early 20th century, the area surrounding Mineral King and Timber Gap was included in the newly formed Sequoia National Forest. There were, and still are, many parcels of private property in the area that remain as inholdings surrounded by federal land. In the late 1950's the area was threatened with a Walt Disney-sponsored idea to create a ski area at Mineral King. The controversy over the proposal carried on for nearly 20 years, until the 12,500-acres of the Mineral King region were incorporated into Sequoia National Park by a 1978 act of Congress.

Today the area is home to many private cabin inholdings, a small resort, and several trailheads into the major backcountry areas of Sequoia National Park. The foxtail pine forest above Timber Gap is well known to subalpine tree lovers due to the presence of some very large foxtails. The largest-known foxtail is found here, measuring in with a 2.8-m DBH and a height of nearly 22 meters.

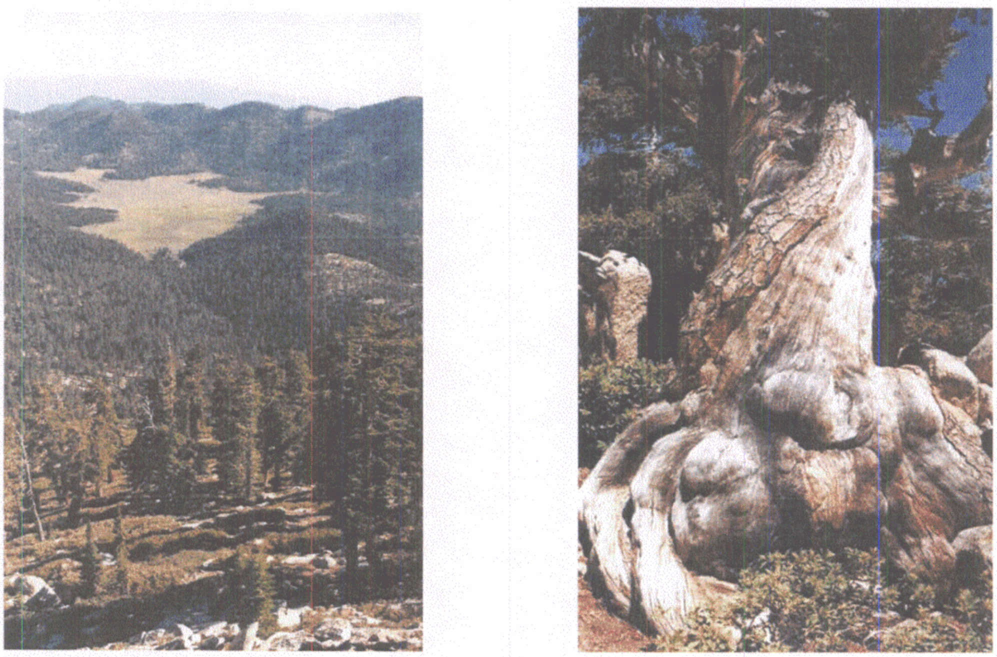


The author standing next to and on very large foxtails (left), and Mineral King valley from Timber Gap.

SIRRETTA

The foxtail pine stand of Sirretta Peak was an unknown botanical unit until less than 35 years ago. Located in the Sequoia National Forest, it was not until 1966 that their presence was detected. The stand is located 40 km south from the closest other foxtails at Olancha Peak, just south of the Cottonwood area. It was quite a surprise to find these trees at such a low elevation and latitude, and in competition with a suite of other conifers. Their discovery has led to a plethora of questions about the evolutionary history of this group, and how it came to be established in such an atypical location.

The area surrounding Sirretta Peak is located within the Ernest C. Twisselman Botanical Area, named for a famous local rancher and amateur botanist. Like the Foxtail Pine Research Natural Area near Trail Peak, the designation carries no special protection, but shows that the area is recognized as a significant botanical unit. Oddly enough, the foxtail pines of Sirretta Peak are also located in an off-road vehicle use area, with a trail cutting directly though the center of the Sirretta Peak stand (OHV trail 34E12). However, in visits to the area no noticeable impacts were seen. The trail was in good condition and was less incised than many foot trails observed elsewhere in the Sierras. Grazing is common in the Big Meadow area two miles south of Sirretta Peak. Barbwire was found at Sirretta Pass that suggested some past animal control (likely drift fences), but no recent evidence of cattle or pack animals was found.



A view south from Sirretta Peak to Big Meadow (left), and a gnarled old foxtail at Sirretta Pass.

The Dome Land Wilderness Area is directly east of Sirretta Peak, and was the epicenter of the 65,000-acre "Manter Complex" wildfire of July 2000. The fire burned within a few miles of Sirretta Peak, but luckily the prevailing westerlies kept the fire away from the unique botanical features of Sirretta.

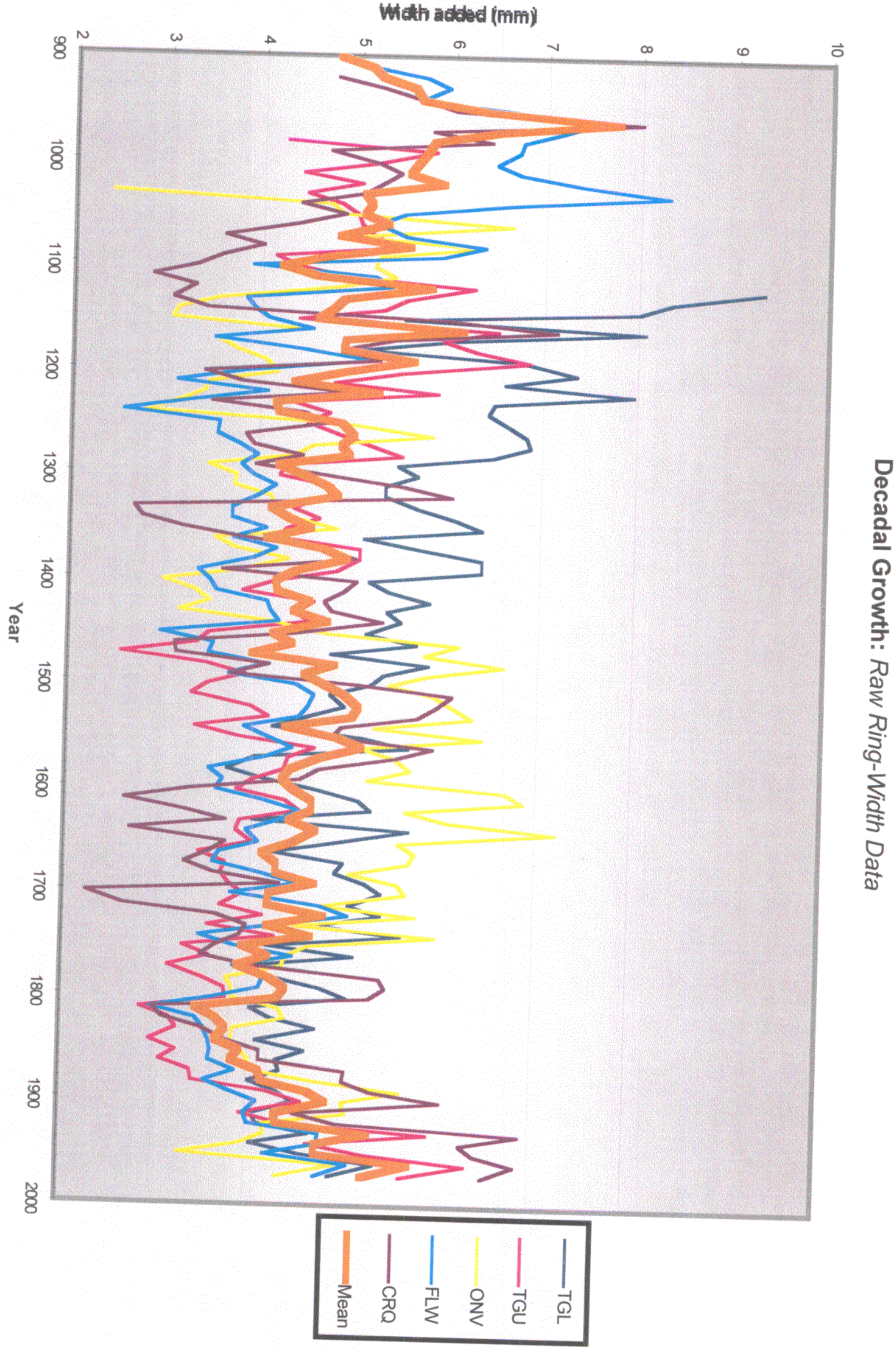
APPENDIX II

Study site photographs from summer and fall 2000.

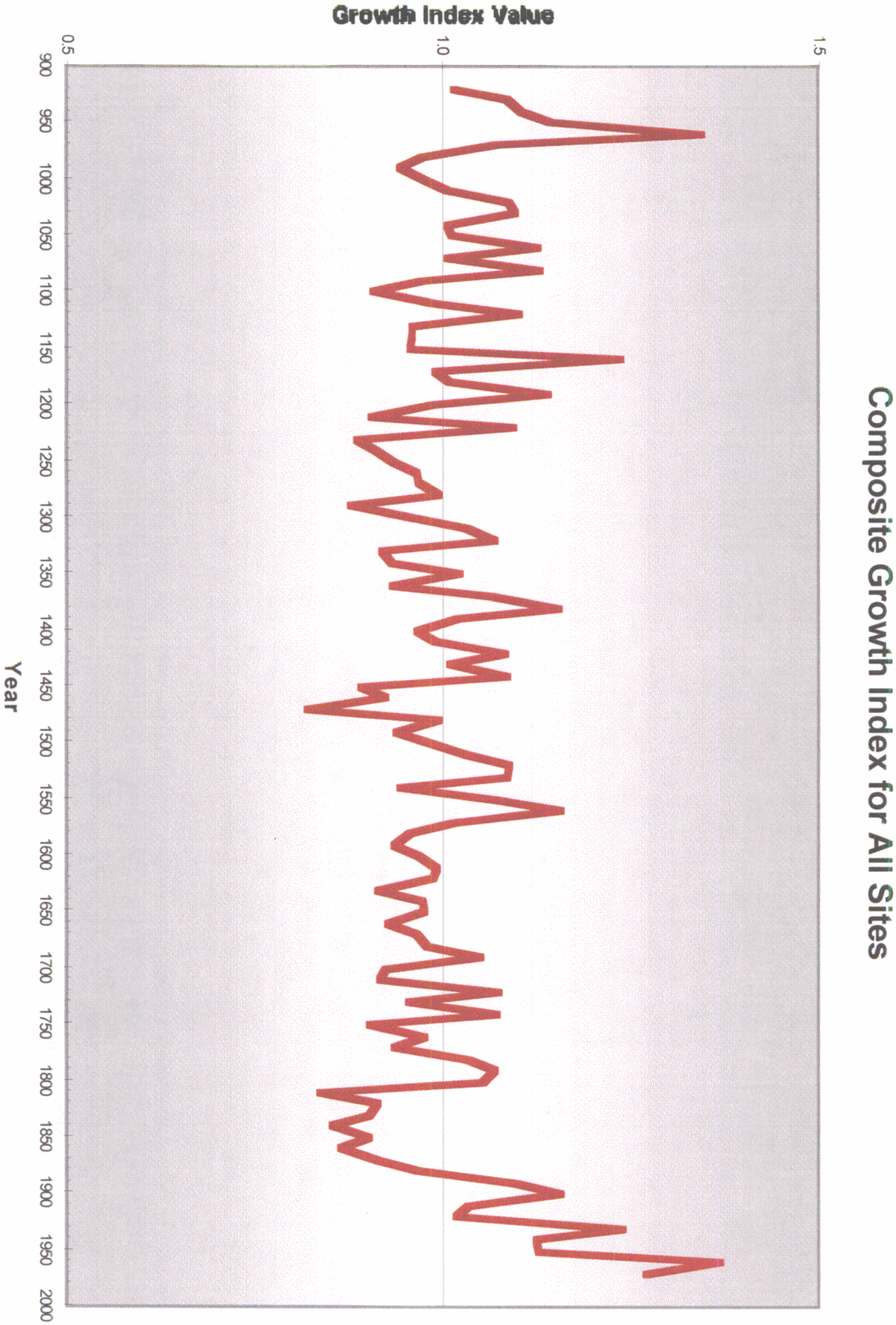
Content: Thumbnails of photographs taken over study period (appox. 50 available for digital viewing).

Note: Available for interactive document and web page only, not for this printed document.

Appendix III



Appendix IV


Composite Growth Index for All Sites
Growth Index Value
0.5
1.0
1.5
Year
900
950
1000
1050
1100
1150
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